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THE ROLE OF VISUAL STABILITY IN REPRESENTATIONS OF PRE- AND POST-SACCADIC OBJECTS

by

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CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

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To Suzi & Turi.

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ABSTRACT

During everyday scene viewing, the information received by the visual system is frequently disrupted: Objects are often occluded by other objects, and sensory processing is interrupted by eye, head, or body movements. The visual system is extremely efficient at correcting for these interruptions and in establishing object correspondence and perceptual continuity. At the end of this correspondence process, the visual system is left with two representations of an object: The initial representation and the one acquired after the disruption. In the present dissertation, I investigated the mechanisms by which the visual system reconciles these discontinuous inputs to give us a perception of a smooth and stable visual world.

To achieve this, I ran four experiments in which participants were presented with a colored saccade target, and instructed to remember its color before executing the saccade. On some trials, the color of the saccade target was changed to a new value during the saccade. Participants were asked to report either the pre- or post-saccadic color value in a continuous report task. Object continuity was manipulated in two ways. The target blanking paradigm served as the main manipulation of stability: On half the trials, the target was removed from the screen during the saccade, disrupting object continuity. In addition, the magnitude of color change was used as a secondary manipulation of visual stability. The color report data were fit with probabilistic mixture models. First, there was no evidence for integration of pre- and post-saccadic feature values into a composite representation. Instead, on a majority of trials participants could successfully retain and report both pre- and post-saccadic states of the target object. Further, these two states dynamically interacted with each other, resulting in their feature values systematically shifting toward each other. Lastly, when reporting the pre-saccadic color, participants were more likely to incorrectly report the post-saccadic color under conditions of visual stability versus instability, supporting a probabilistic overwriting mechanism. Together, these results are more consistent with an object-based model, rather than an image-based model of representational updating. Although the present study only focused on transsaccadic updating mechanisms, similar mechanisms are likely to be functional in many common situations where the visual system needs to establish perceptual continuity across disruptions and changes.

PUBLIC ABSTRACT

People frequently move their eyes to gather information about the objects in the world. The most common types of eye movement are *saccades*, rapid eye rotations to extract detailed visual information. During each saccade, the visual input is disrupted; thus, creating a problem for our visual system. In the current project, I investigated how the visual system integrates information we perceive before and after a saccade to enable the perception of a continuous visual environment. To determine the underlying mechanisms of this updating process, participants were presented with a saccade target, and instructed to execute a saccade to it. The continuity of the target was manipulated by both removing it from the screen and by the changing its color during the saccade. At the end of each trial, participants reported either the first (pre-saccadic) or the second (post-saccadic) color. The results revealed two main mechanisms of representational updating. First, color value of the pre-saccadic representation was more likely to be replaced by the post-saccadic color value when the target was perceived as continuous, compared to when its continuity was disrupted. This overwriting was not an automatic process; however, because participants could successfully report both pre- and post-saccadic colors on a majority of trials. Second, pre- and post-saccadic color reports were shifted toward the other color value, indicating a dynamic interaction between them. These results provide evidence for two main

mechanisms by which the visual system updates object representations when faced with perceptual discontinuity.

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INTRODUCTION

The human visual system faces many challenges during everyday scene viewing. In particular, the information reaching our visual system is disrupted by our eye, head, and body movements. The most frequent disruption occurs during saccadic eye movements. We move our eyes 2-3 times per second to extract high-resolution information from the visual environment. However, every time we execute a saccade, the visual system faces two problems: retinal blur and maintaining space constancy. First, during each saccade, the projected image sweeps rapidly across the retina, yet we do not perceive a blurred image of the world. This insensitivity to visual input during saccade execution is explained by an active suppression mechanism, termed saccadic suppression (for reviews, see Higgins & Rayner, 2015; Matin, 1974; Wurtz, 2008). The second problem is space constancy, which refers to perceiving stable objects across saccades even though the images of those objects are shifted on the retina after each saccade (Bridgeman, Van der Heijden, & Velichkovsky, 1994; Matin, 1974). Despite these retinal shifts, the visual system is extremely efficient in differentiating saccade-induced changes from actual environmental changes, leading us to perceive a smooth, continuous visual world. The mechanism behind establishing a stable environment from discontinuous input has been discussed for centuries (Alhazen, 1083).

In general, there are two main views of transsaccadic stability based on the nature of the scene representation: image-based and object-based. According to image-based accounts, the perception of a continuous visual environment is created by the integration of relatively low-level image properties across the entire visual field (e.g., Brietmeyer, Kropfl, & Julesz, 1982; Duhamel, Colby, & Goldberg, 1992; Jonides, Irwin, & Yantis, 1982). Alternatively, object-based accounts propose that transsaccadic stability depends on a local representation of the saccade target object. Instead of a global integration process, stability is achieved by a comparison operation, in which the pre-saccadic properties of the target object are compared with the post-saccadic information near the saccade landing position (e.g., Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; Deubel, Schneider, & Bridgeman, 1996; Hollingworth, Richard, & Luck, 2008).

In the following section, I will first review these two accounts of transsaccadic stability and behavioral studies that test them. Then, I will move to recent neuronal findings on receptive field remapping and how they relate these image-based and object-based accounts. As will be discussed below, current evidence suggests that transsaccadic stability is achieved with an object-based process which consults the local information of the saccade target object. In the present dissertation, I present six experiments in which I investigated the underlying mechanisms of transsaccadic updating. Specifically, I asked how the visual system reconciles multiple representations of the same object obtained during each fixation to generate a continuous representation of the visual world. At the broader level, examining the processes by which representational updating occurs will inform us about the general updating mechanisms by which the visual system creates a coherent perception of a continuous visual environment when faced with changes in input.

Theories of transsaccadic perception and stability

Image-based accounts

Image-based accounts propose that the visual system represents and integrates the visual scene in a point-by-point manner, whereby every element of the scene is integrated and updated independently. An important assumption of these accounts is that the visual system encodes and uses the direction and amplitude of each saccade to fuse the pre- and post-saccadic images into a single percept (Banks, 1983; Brietmeyer et al., 1982; Jonides et al., 1982; McConkie & Rayner, 1976). This integration process is suggested to be performed for the entire visual scene, resulting in global fusion of the visual field after every saccade. Further, transsaccadic integration of information is completed in a buffer that is organized in terms of external space, a *spatiotopic fusion hypothesis* (Irwin, 1992c).

Several predictions can be drawn from the image-based accounts. First, if transsaccadic perception depends on a global integration process, participants should be able to fuse pre- and post-saccadic information to form a composite representation. Second, if high-resolution images are retained across saccades, then participants should demonstrate robust ability to detect changes that occur anywhere in a scene. Previous studies have found evidence contradicting each of these predictions.

Initially, studies that tested the global integration prediction found that participants could successfully fuse visual images across saccades, supporting image-based accounts (Banks, 1983; Brietmeyer et al., 1982; Jonides et al., 1982; McConkie & Rayner, 1976; Wolf, Hauske, & Lupp, 1978, 1980). However, later studies showed that those findings were due to artifacts of the CRT monitor phosphor persistence and that low-level visual information is in fact not integrated across saccades in this manner (Bridgeman & Mayer, 1983; Irwin, Brown, & Sun, 1988; Irwin, Yantis, & Jonides, 1983; Irwin, Zacks, & Brown, 1990; McConkie & Zola, 1979; McConkie, Zola, Blanchard, & Wolverton, 1982; O'Regan & Lévy-Schoen, 1983; Rayner & Pollatsek, 1983). For instance, it has been shown that participants cannot integrate two dot matrices across saccades (Irwin et al., 1988). In their experiment, Irwin et al. (1988) presented participants with two 3x3 matrices separated by a saccade (see Figure 1.1). In each matrix, four of the nine possible cells were filled with a dot, such that integrating both matrices would result in a single matrix with eight filled cells and one empty cell. Participants’ task was to report the location of that empty cell. When the matrices were presented at the same screen location before and after the saccade, performance was no better than chance, indicating that there was no spatiotopic visual integration across the saccade. Similar results have been reported in other transsaccadic integration tasks (Bridgeman & Mayer, 1983; Irwin, 1992b; Irwin et al., 1983; O'Regan & Lévy-Schoen, 1983; Rayner & Pollatsek, 1983). Together, these studies suggest that integration of information in terms of objects' spatiotopic locations does not seem a plausible mechanism for establishing stability across saccades.

Further evidence against such a global integration process comes from transsaccadic change detection studies. As mentioned above, if the visual system maintains detailed information about the objects across saccades, then any transsaccadic change should be easily detected. Contrary to this idea, studies have shown that observers tend to miss significant changes that occur during the saccade (e.g., Bridgeman & Stark, 1979). For instance, spatial displacements of the saccade target object are usually not detected unless the displacement is greater than 1/3 of the saccade itself (Bridgeman, Hendry, & Stark, 1975). Similar results were also reported in studies that used naturalistic scenes. Changes in object features (e.g., size, orientation, spatial position, color) often went unnoticed if they occurred during a saccade (Grimes, 1996; Henderson & Hollingworth, 1999, 2003; McConkie & Currie, 1996).

Reading studies have also found evidence against sensory integration (McConkie & Zola, 1979; Rayner, McConkie, & Zola, 1980). For instance, McConkie and Zola (1979) tracked participants eye movements while they read a text that consisted of words with AlTeRnAtInG cAsE lEtTeRs. Multiple times during reading, the case was reversed for each letter while participants were executing a saccade. Not only did participants fail to detect these changes, eye movement patterns were not affected by case change. If low-level sensory information is integrated and fused spatiotopically across saccades, case changes should have disrupted the reading process, and participants should have had great difficulty completing this task. In sum, there is substantial evidence that transsaccadic visual stability is not achieved with an image-based mechanism by which the pre- and post-saccadic representations are globally fused into a single image.

Object-based accounts

In contrast to the image-based accounts that explain visual stability by a global integration of pre- and post-saccadic visual representations, other accounts propose that the transsaccadic representation of the visual world is object based (Bridgeman et al., 1994; Currie et al., 2000; Deubel, Bridgeman, & Schneider, 1998; Hollingworth et al., 2008; McConkie & Currie, 1996). Specifically, for visual stability operations, only the most salient and relevant part of the scene, the saccade target, is retained across the saccade. Transsaccadic stability is achieved by a comparison process in which these retained properties are compared against the properties of objects near the landing position of the saccade. Under this view, there are three processing stages of stability operations. First, as the visual system selects a saccade target, attention is covertly shifted to that object before saccade execution (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Second, this attention shift leads to preferential encoding (Irwin, 1992a; Irwin & Andrews, 1996; Irwin & Gordon, 1998; Tas, Luck, & Hollingworth, 2011) and maintenance of the saccade target's features in visual working memory (VWM) (Hollingworth & Luck, 2009; Hollingworth et al., 2008; T. Moore, Tolias, & Schiller, 1998). Finally, after the saccade is completed, remembered properties of the saccade target object are compared with the properties of objects near the saccade landing position.

Visual stability is established if there is a match between the remembered and the newly fixated properties. If, however, there is a discrepancy between the remembered target representation and the features of the objects at or near the saccade landing position, the visual system will not be able to establish object correspondence, and stability will be disrupted. It should be noted that stability operations may not be exclusively based on the saccade target object. Other attended objects near the saccade landing position can be used to establish transsaccadic object correspondence when they become task relevant (Deubel, 2004; Deubel et al., 1998; Germeys, de Graef, Panis, van Eccelpoel, & Verfaillie, 2004; Germeys, De Graef, & Verfaillie, 2002; Prime, Tsotsos, Keith, & Crawford, 2007; Verfaillie & De Graef, 2000).

To explore the role of the saccade target object in transsaccadic stability, Currie and colleagues (2000) assessed participants' change detection performance while they viewed pictures of natural scenes. The changes occurred as participants executed a saccade to a target object. On a given trial, one of three changes could occur. In the *object shift* condition, the saccade target object was shifted and the rest of the scene remained stationary. In the *all shift* condition, the entire image was shifted. Lastly, in the *background shift* condition, everything in the image except the target object was shifted. In each of these conditions, the shift could be either to the left, right, up, or down. There was also a control condition in which no change was introduced to the picture. All four types of shifts were approximately 1/3 of the length of the saccade. The authors hypothesized that if transsaccadic stability is established using the local information about the saccade target object then participants should easily detect the changes in the object shift and all shift conditions, while being relatively insensitive to changes in the background shift condition. If, however, global image information is stored and integrated across saccades, change detection performance should have increased as the number of changed features increased. Therefore, image-based accounts predict better change detection performance for the background shift and all shift conditions than for the object shift condition.

The Currie et al. (2000) results supported the object-based account. Change detection accuracy was similarly high for object (83%) and all shift (74%) conditions. However, only 34% of the background changes were detected. This finding is notable, because in the background shift condition, every pixel in the picture was shifted, except for the saccade target object. High sensitivity to target shifts relative to background shifts suggests that saccade target information was strongly prioritized for retention across the saccade and for comparison after the saccade.

Although the priority of the saccade target in transsaccadic perception is well established, it can be surprisingly difficult for participants to access extremely precise features of the saccade target object. In the study of Currie et al. (2000), the magnitude of the target displacement was approximately 1/3 of the saccade amplitude. For smaller shifts, visual system is highly insensitive to intrasaccadic position displacements of the saccade target, even when the target is the only object on the screen (Bridgeman et al., 1975). In standard displacement detection experiments, a small target disk is first displayed at central fixation. After a delay, the disk is shifted horizontally (see Figure 1.2). Participants are instructed to execute a saccade to that peripheral disk. During the saccade, the disk is shifted for a second time, either to the same or the opposite direction of the first saccade. The task is to report the direction of this second shift in relation to the saccade direction (forward or backward). In this standard condition (no-blank), the general finding is that participants' displacement detection performance is poor, unless the target displacement exceeds 1/3 of the distance of the saccade (top-left panel of Figure 1.3) (Bridgeman et al., 1975). How, then, can the saccade target object be preferentially processed, but participants are often insensitive to its spatial displacements? These seemingly contradictory findings could be explained by the updating of the properties of the saccade target object after the saccade. Specifically, when visual stability is established, the pre- and post-saccadic properties will be mapped to the same object, which could lead to replacement of the pre-saccadic properties with the post-saccadic ones. This updating process would prevent conscious access to pre-saccadic location for report, resulting in poor displacement detection performance. When the pre- and post-saccadic properties are sufficiently different and cannot be mapped to the same object, the visual system would create a new object representation for the post-saccadic object, the pre- and post-saccadic properties would be associated with different object representations, and the latter would not necessarily overwrite the former. In this case, pre-saccadic features of the saccade target should be easily accessible.

Support for this updating proposal comes from studies that used a modified version of the target displacement paradigm (Demeyer, De Graef, Wagemans, & Verfaillie, 2010a; Deubel et al., 1996; Tas, Moore, & Hollingworth, 2012). In their influential study, Deubel et al. (1996) used the same transsaccadic displacement detection task as Bridgeman et al. (1975) with one modification. In addition to the standard condition (no-blank), another condition was included in which the continuity of the saccade target object was disrupted (blank). In these blank trials, the target object was removed from the screen for a short period (about 250 ms) during the saccade to the target (blank condition in Figure 1.2). After the blank, the target disk was presented at its displaced location. Blanking the target caused the eyes to land on an empty screen after the saccade was completed, followed by the appearance of the target. In this blank condition, displacement detection performance was remarkably improved compared to the no-blank condition (top-right panel of Figure 1.3). A plausible explanation for this increased displacement detection is the disruption of object continuity when the saccade target was blanked. In the no-blank condition, pre- and post-saccadic representations were mapped to the same object; therefore, the pre-saccadic information was updated and overwritten by the post-saccadic information. In contrast, blanking the object resulted in the perception of two distinct objects (pre- and post-saccadic). Thus, the pre-saccadic information was not updated with the post-saccadic information, enabling access to precise information about the pre-saccadic position of the target (Demeyer et al., 2010a; Tas, Moore, et al., 2012). If this interpretation is correct, then any manipulation that disrupts target continuity should similarly result in increased sensitivity to spatial displacements.

To test this idea, Tas, Moore, et al. (2012; also see Demeyer et al., 2010) added a third condition in which they manipulated the surface features of the target object during the saccade. In their first experiment, the contrast polarity of a target disk was changed during the saccade at the same time as the spatial displacement took place (polarity-change condition, Figure 1.2). Therefore, this condition was identical to the no-blank condition in terms of the object's spatiotemporal properties, but the pre- and post-saccadic disks had different surface features. This simple surface feature change significantly enhanced spatial displacement detection accuracy compared to a no-change condition. Complete removal of the target, a blank, still led to the highest level of displacement detection, however (bottom-left panel of Figure 1.3). In a second experiment, they used pictures of round real-world objects (e.g., basketball, clock, coin). On change trials, multiple surface features of the object as well as its identity were changed (object-change condition, Figure 1.2). They found that changing the object resulted in similar sensitivity to spatial displacement as blanking the object entirely (bottom-right panel of Figure 1.3). That is, as the number of surface feature changes increased, displacement detection performance increased. These results suggest that the visual system encodes and compares the properties of the pre- and post-saccadic target objects. Mismatch between these representations results in disruption of object continuity. In addition, these displacement detection studies suggest that the visual system has a high tolerance for discrepancy when making the continuity judgment. For location information, the object is perceived as stable unless it is moved approximately 1/3 of the executed saccade (Bridgeman et al., 1975). Similarly, Tas, Moore, et al. (2012) found that changing the contrast polarity of the target did not disrupt stability as strongly as blanking, indicating that the visual system is biased to establish stability, and can be tolerant to quite substantial surface feature changes.

To recapitulate, behavioral studies have shown that visual stability is established in an object-based manner, with a local evaluation of the saccade target object's features used to establish transsaccadic object correspondence and hence visual stability across saccades. However, this broad consensus on the basis of behavioral studies has been challenged by neuronal evidence, which has been interpreted as consistent with image-based integration. In the next section, I will first review key findings indicating that neurons shift their receptive fields in anticipation of a saccade, a process known as *predictive remapping*, and how this phenomenon has been interpreted as supporting global, image-based integration. I will then review recent research suggesting that the neuronal evidence is in fact more consistent with object-based theories than with image-based theories.

Predictive Remapping

Dynamic Receptive Fields. When the motor areas of the brain generate a signal indicating a saccade, a copy of that signal is sent to the visual areas. This copy signal is called corollary discharge (CD) or efference copy (Sperry, 1950; von Holst & Mittelstaedt, 1950). CD informs the neurons in the visual processing areas about the amplitude and direction of the upcoming saccade[1] (Sommer & Wurtz, 2008). This information about the saccade could plausibly be used to remap the pre-saccadic sensory representation so as to align it with the future (post-saccadic) representation, allowing for spatial continuity in low-level sensory processing and, thereby, the experience of visual stability (for reviews, see Bridgeman, 2007; Grüsser, 1995).

Supporting this idea, neurons in some areas of the primate brain shift their receptive fields (RFs) before a saccade. In their seminal study, Duhamel, Colby, and Goldberg (1992) recorded activity of neurons in lateral intraparietal area (LIP) while monkeys prepared and executed a saccade (see Figure 1.4). As expected, neurons increased their firing rates for stimuli presented in their current RF (Figure 1.4A). Importantly, the same neurons also increased their firing rates for stimuli which would

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[1] Sommer and Wurtz (2004, 2008) proposed a possible CD pathway that ascends from the medial dorsal nucleus (MD) of the superior colliculus to frontal eye fields in frontal cortex.

fall in their future receptive field (FF) after the completion of the saccade (Figure 1.4B). This increased activity started about 80 ms before the monkey executed the saccade, demonstrating that the neurons shifted their RFs in anticipation of a change in gaze. These receptive field shifts prior to saccade execution are termed *predictive remapping*. The authors also found that covert shifts of attention do not result in similar RF shifts, suggesting that this predictive remapping mechanism is specific to saccade execution. Later studies replicated these results in LIP (Batista, Buneo, Snyder, & Andersen, 1999; Colby, Duhamel, & Goldberg, 1996; Duhamel et al., 1992; Heiser & Colby, 2006; Kusunoki & Goldberg, 2003), as well as extending them to other areas in the brain, such as frontal eye fields (FEF) (Sommer & Wurtz, 2006; Umeno & Goldberg, 1997, 2001), superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995), early visual areas such as V4 (Tolias et al., 2001), V3 and V2 (Nakamura & Colby, 2002), and even V1 (Khayat, Spekreijse, & Roelfsema, 2004). Further, Sommer and Wurtz (2006) found that inactivating a part of the pathway that carries CD (specifically, medial dorsal nucleus of superior colliculus, MD) significantly reduced the remapping response at the FF in FEF neurons, indicating that CD is necessary for such RF shifts.

In summary, there is substantial evidence that neurons shift their receptive fields in anticipation of a saccade. The key challenge is to explain how remapping can be responsible for establishing transsaccadic stability. Schneegans and Schöner (2012) presented a dynamic field model to account for the relationship between the neural mechanisms of remapping and perception of visual stability. Although their model successfully captured many behavioral findings, to date, there is no direct evidence demonstrating the functional neuronal mechanisms in primates. Wurtz (2008) proposed that one way to demonstrate a causal relationship is to show that inactivation of MD also results in decreased perception of visual stability. Such a study is tricky to design, because the results would depend on the operationalization of perception of stability in monkeys. Although a functional relationship between neural remapping and stability has yet to be established, researchers have proposed two main hypotheses by which predictive remapping might plausibly support visual stability: image-based integration and object-based comparison.

Image-based integration. According to these newer image-based accounts, the predictive shift of neuronal activation before a saccade transfers low-level feature information from the neuron's current RF to its FF, resulting in pre- and post-saccadic features being integrated across the saccades. This way, information that is received retinotopically can be represented in spatiotopic coordinates (e.g., Hall & Colby, 2011; Melcher, 2005). This idea provides a neural explanation for how image-based integration can be achieved. According to this view, remapping is done across the entire scene, resulting in a global integration process.

Empirical evidence for this image-based integration has been reported in adaptation aftereffect studies where the low-level visual properties are shown to be remapped across saccades. In a typical adaptation aftereffect study, participants' perception of a test stimulus is measured after they were exposed to an adapter stimulus. Adaptation aftereffects are negative aftereffects, such that the test stimulus is perceived as being repelled from the adapter stimulus value (Gibson, 1937). For instance, in the case of tilt aftereffect, after being adapted to a grating tilted to the right, participants usually perceive a neutral test stimulus as tilted to the left (He & MacLeod, 2001; Parker, 1972). Melcher (2005) used this method to test whether adaptation aftereffects can be transferred across the saccade. The idea was that if low-level feature information is remapped across saccades, then after being adapted to a stimulus, RFs of the adapted neurons will shift to their FF location. In this case, the adaptation will move to the neurons' FF after the saccade, resulting in a spatiotopic aftereffect. Evidence for such feature transfers across saccades would then support image-based transsaccadic integration.

In Melcher's experiments, an adapter was presented at fixation (Figure 1.5) for an extended period of time. Then, the fixation cross moved to a new location, and participants were to execute a saccade. Finally, the test stimulus was presented either at the same location as the adapter (spatiotopic) or at a different location (control).

Importantly, aftereffects were present for orientation, shape, and face stimuli when the test stimulus spatiotopically matched the adapter. In line with predictive remapping, similar spatiotopic aftereffects were also found for targets presented at the saccade target's location prior to saccade execution, rather than at the end of the saccade (Biber & Ilg, 2011; Melcher, 2007). These results were taken as evidence that low-level, sensory states are integrated across the saccades (Melcher, 2005, 2007, 2008, 2009).

Later studies, however, challenged this integration account. For instance, several studies have failed to replicate low-level information integration in spatiotopic coordinates, but instead showed strong retinotopic aftereffects, refuting the spatiotopic integration account (Afraz & Cavanagh, 2009; Knapen, Rolfs, & Cavanagh, 2009; Knapen, Rolfs, Wexler, & Cavanagh, 2010; Mathôt & Theeuwes, 2013; Wenderoth & Wiese, 2008). Further, Knapen et al. (2009) argued that the spatiotopic effects found in Melcher studies may be due to spreading of the adaptation effect to a wider area. Generally, after being adapted to a stimulus, the adaptation aftereffect is strongest at the exact adapter location (spatiotopic + retinotopic). However, weaker aftereffects can also be seen at locations other than the adapter location. This type of non-location-specific aftereffects, also called phantom aftereffects, has been widely demonstrated in motion perception (Snowden & Milne, 1997; Von Grünau & Dubé, 1992; Weisstein, Maguire, & Berbaum, 1977). Knapen and his colleagues hypothesized that with a saccade, these non-location-specific aftereffects may move; therefore, these results may be mistakenly interpreted as spatiotopic aftereffects. Studies that carefully measured retinotopic, spatiotopic, and non-location-specific aftereffects replicated strong retinotopic aftereffects. Importantly, similar magnitude spatiotopic and non-location-specific aftereffects were also observed, indicating that earlier spatiotopic reports were in fact not purely spatiotopic (Knapen et al., 2009; Knapen et al., 2010). These results suggest that it is unlikely that visual stability is established by integrating pre- and post-saccadic information.

Object-based comparison. Another explanation of how remapping may contribute to transsaccadic stability is that it supports a comparison mechanism (instead of an integration mechanism) between pre- and post-saccadic properties (Crapse & Sommer, 2008; Heiser & Colby, 2006; Wurtz, 2008; Wurtz, Joiner, & Berman, 2011). Specifically, receptive field shifts prior to the saccade gives the neuron a head start in processing the information at the target (FF) location (Mathôt & Theeuwes, 2011). This way, the visual system can generate a prediction about the expected visual stimulus after the saccade. After the completion of the saccade, this expected stimulus is compared with the currently fixated stimulus. It should be noted that the exact mechanism by which this comparison is achieved is not yet clear (Bays & Husain, 2007).

Such a comparison can only occur if the activation at the FF location actually creates a prediction about the upcoming stimuli. To test this idea, previous studies used cueing paradigms. The idea is that if attention is shifted to a location, processing of stimuli presented at that attended location will be facilitated. If a saccade is executed following the attentional shift, then the neuron's RF will be remapped to their FF, showing enhanced processing of information appearing at their FF prior the saccade.

In one study, Mathôt and Theeuwes (2010a, see also Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011) instructed participants to fixate on a gray dot (Figure 1.6). Then, three additional dots were presented, and one of them was cued by changing its color. Participants were instructed to execute a saccade to the cued dot. At the same time as the saccade target cue, a sudden onset object (a square) was presented on the screen, leading to shifts of attention to that location. After participants completed the saccade, a target line was briefly presented and participants' task was to report the orientation of this line. The target line could appear at the same spatial location as the cue (spatiotopic), the same location relative to the fixation (retinotopic), or one of the two control locations (bottom panel, Figure 1.6). Reaction times for the orientation task were faster when the target line appeared at the spatiotopic location compared to its control location. Importantly, similar facilitations were found for targets that appeared at the retinotopic location. Furthermore, this retinotopic facilitation was present when the line target was presented before the saccade, suggesting that attention remapping is predictive. The researchers suggested that these retinotopic effects are evidence for *remapping of attention*: Attention shifts to its future retinotopic positon before the saccade, enabling neurons to obtain information about the stimuli to create a prediction about the post-saccadic perception.

Additional evidence for remapping of attention was found in saccadic inhibition of return (IOR) studies (Mathôt & Theeuwes, 2010b). IOR refers to the finding that participants are slower to orient their attention to a previously attended location (Posner & Cohen, 1984). Mathôt and Theeuwes (2010b) measured the time course of attention remapping by cueing participants' attention to an empty location before they executed a saccade to a displaced dot. After a variable time interval, participants executed a saccade to a new target. The stimulus onset asynchrony (SOA) between the attention cue and the new saccade target was manipulated. In addition, the location of the saccade target was manipulated in relation to the cue (spatiotopic, retinotopic, or control). Participants were slower to execute a saccade (i.e., significant IOR) to the retinotopic locations for short SOAs. Importantly, as the SOA increased, the magnitude of retinotopic IOR decreased and spatiotopic IOR increased. Earlier retinotopic IOR indicates that the neurons first start inhibiting their conventional RFs. After the remapping is complete, inhibition is switched to the spatiotopic coordinates, leading to

IOR at the spatiotopic locations. Together with other findings showing enhanced processing of information at the future retinotopic location (e.g., Golomb, Chun, & Mazer, 2008; Golomb, Marino, Chun, & Mazer, 2011; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), these results are taken as behavioral evidence for predictive remapping of attention across saccades.

One way predictive remapping of attention can support stability is to facilitate the processing of the attended objects before the saccade is executed by creating a prediction of post-saccadic information. This facilitation, however, will be selective because only stimuli that are under the current focus of attention will be remapped (Gottlieb, Kusunoki, & Goldberg, 1998). If the predicted information matches the post-saccadic information, visual stability will be established (Wurtz et al., 2011). Although it sounds plausible, the predictive remapping idea has yet to define a mechanism that is responsible for the comparison process (Bays & Husain, 2007). The current evidence only shows that the neurons display enhanced activation for the saccade target object. However, merely showing that neurons respond to the same stimulus twice cannot explain if and how a comparison between the pre- and post-saccadic can be achieved (Higgins & Rayner, 2015).

Recently, Zirnsak, Steinmetz, Noudoost, Xu, and Moore (2014) has provided evidence that challenged the involvement of the receptive field shifts in any type of remapping operation discussed above. According to their proposal, neurons do not necessarily shift their receptive fields to their FFs. Instead, the receptive fields converge toward the saccade target object. Using a similar design in previous remapping studies, Zirnsak et al. (2014) trained monkeys to execute a saccade to a target and measured activations in FEF. In contrast to the previous studies, the specific locations of the receptive fields were measured by presenting a large array of visual stimuli (rather than a single target object). This way, the authors could measure activity of a wide range of neurons and more importantly, the direction of their receptive field shifts. The results showed that the receptive fields do not systematically shift toward their FF location. Instead, they shift toward the saccade target location, showing a compression of visual space (Figure 1.7). Previous studies have shown behavioral evidence for compression of the visual space around the saccade target. Specifically, if a probe object is flashed around the time of a saccade, the perceived location of the probe is shifted toward the saccade target object, indicating compression (Hamker, Zirnsak, Calow, & Lappe, 2008; Kaiser & Lappe, 2004; Ross, Morrone, & Burr, 1997). Considering both behavioral and neuronal findings, Zirnsak and Moore (2014) proposed that RFs are not aligned with their FFs (i.e., remapped) as initially proposed. Rather, they converge toward the saccade target object (or a task-relevant, salient object in the visual field) for the purposes of acquiring information about that object.

These results are inconsistent with the idea that visual stability is achieved with a global predictive remapping mechanism by which visual images are integrated across saccades. Instead, the convergence of the RFs toward the location of the saccade target can be conceptualized as the allocation of perceptual resources to the target object. This, in turn, may support preferential encoding of the saccade target features for post-saccadic comparison, as proposed by behavioral object-based accounts (Currie et al., 2000; Deubel, Schneider, & Bridgeman, 2002; Hollingworth et al., 2008; Tas, Moore, et al., 2012).

Predictive Remapping Summary. Evidence for dynamic receptive fields of neurons in visual areas of the brain is well established. However, the nature of receptive field changes is not fully understood (for summaries of different proposals, see Cavanagh, Hunt, Afraz, & Rolfs, 2010; Wurtz, 2008; Zirnsak & Moore, 2014). In addition, there is no direct evidence that predictive remapping is involved in visual stability, because it is not clear yet how comparisons between the RF and FF activations are achieved (Higgins & Rayner, 2015). Importantly, recent findings revealed that RFs converge toward the saccade target location, rather than shifting toward their FF (Zirnsak & Moore, 2014). This convergence mechanism is likely to be functional in encoding the properties of the saccade target object, as held by object-based accounts of transsaccadic perception.

Summary

Current evidence suggests that visual stability is established in an object-based manner rather than with an image-based integration mechanism. Specifically, the properties of the saccade target object are encoded and retained across the saccade and then compared with the post-saccadic properties at the saccade landing position. Object-based accounts successfully explain the conditions under which visual stability will be disrupted: When the object at the saccade landing position cannot be interpreted as the original saccade target object, then the target (and visual world in general) will not be perceived as continuous. In this situation, pre- and post-saccadic features will be mapped to different objects. If, however, the pre- and post-saccadic features match, the target will be perceived as continuous, and visual stability will be established. One limitation of this account is that it does not offer any explanation for how pre- and post-saccadic representations are reconciled, which will be the main focus of the current dissertation.

Transsaccadic updating

The goal of the human visual system is to internally represent an accurate description of the visual environment so that we can successfully guide our actions. However, the high-resolution information the visual system receives at a given time is limited to the area around fixation. To resolve this limitation, we constantly shift our gaze and sample information from the outside world. This continuous fixation-saccade-fixation cycle results in separated representations of the same objects, leaving the visual system with yet another challenge. How does the visual system reconcile multiple representations of the same objects across saccades to generate a seamless perception of the visual world? What is the mechanism by which object information is updated across saccades? The present experiments are designed to directly test this question.

The previous section reviewed theories that explain how the visual system establishes object correspondence across disruptions created by saccades. In the present dissertation, I seek to understand the consequences of establishing transsaccadic stability. When visual stability is established, and the saccade target is perceived as continuous, how is the target's original representation updated with the current one? Previously, Tas, Moore, et al. (2012) proposed that the mechanism supporting transsaccadic updating may be object-based in the same manner as the mechanism that establishes object correspondence. Specifically, they have proposed that a general object-mediated updating mechanism may be responsible for coordinating visual information across saccades and across other forms of disruptions that require an object correspondence mechanism, such as object motion or occlusion.

Object-mediated updating

Object-mediated updating is a form of object-based masking (Enns, Lleras, & Moore, 2009; C. M. Moore & Enns, 2004; C. M. Moore & Lleras, 2005; C. M. Moore, Mordkoff, & Enns, 2007). According to this framework, the representational updating of visual stimuli is completed at the level of object representations. This idea contrasts with an image-level updating mechanism in which every pixel of the scene is updated and replaced with the new information. The distinction between object-based and image-based updating is similar to the distinction between transsaccadic stability based on image-level integration (e.g., Duhamel et al., 1992; Mathôt & Theeuwes, 2010a) and stability based on object-level comparison (e.g., Currie et al., 2000).

Object-mediated updating describes processes by which the visual system either updates the representation of an object or creates a new object representation. If the currently visible properties of an object can be assigned to a previously visible object, then the object will be perceived as the continuation of the previous one. In this case, the previous representation of the object will be updated with its current representation and the initial properties will be replaced by the currently visible properties. On the other hand, if the currently visible properties cannot be assigned to a previously visible object, then object correspondence will fail, and the visual system will create a new object representation with the currently visible properties. Consequently, the properties of the original object will be protected from being overwritten. Thus, according to this framework, the availability of the original properties of an object is modulated by object correspondence operations.

Object-mediated updating has been shown in other situations where the visual system needs to establish object correspondence due to discontinuous input (for a review, see Enns et al., 2009). For instance, C. M. Moore et al. (2007) showed that perception of a smooth, continuously moving object in apparent motion displays can be explained by an object-mediated process. If a stimulus is flashed briefly, its visual features will remain visible for a longer duration than its actual presence on the screen. The duration of this *visible persistence* is reduced if another, similar stimulus is flashed in close spatial and temporal proximity as the first stimulus. This decrease in visible persistence is called motion deblurring (Burr, 1980), and results in the perception of continuous motion from a series of instantaneous presentation of similar stimuli. In these types of apparent motion displays, when two visually similar items are consecutively flashed in close proximity, the visual system maps them to the same object representation and establishes object correspondence. The later state of the object overwrites the earlier state, leading to reduction of the visible persistence and perception of continuous motion. If this reasoning is correct, then disrupting correspondence between the two states should prevent overwriting of visible persistence, the persistence of the first object should extend into the visible presentation of the second, and participants should perceive two objects. To disrupt object continuity, C. M. Moore et al. (2007) manipulated the object's surface features during an apparent motion sequence. They presented disks in a series of adjacent locations, leading to the perception of one disk traveling across the screen (Figure 1.8). On some trials, toward the end of this motion sequence the size of the disk was decreased for one frame. After this salient size change, the continuity of the traveling object was disrupted, and participants consequently reported seeing two objects simultaneously (the persistence of the original large disk, and the smaller disk). These results suggest that when object correspondence is established, the previous state of the object is updated with the later state with an object-based masking process, leading to elimination of visible persistence and perception of one disk moving smoothly across the screen. However, under conditions where correspondence is not achieved due to a mismatch between the initial and new instantiation of the object, a second object representation accounting for the new properties is created, resulting in the perception of two separate objects.

An important aspect of the object-mediated updating framework is that both spatiotemporal and surface feature information are consulted in object correspondence operations. In line with this proposal, previous studies have shown that the visual system flexibly uses both spatiotemporal (Flombaum, Scholl, & Santos, 2009; Mitroff & Alvarez, 2007) and surface feature information like color, shape, size, and luminance (Feldman & Tremoulet, 2006; Hein & Moore, 2012; Hollingworth & Franconeri, 2009; Hollingworth et al., 2008; C. M. Moore & Enns, 2004; C. M. Moore et al., 2007; C. M. Moore, Stephens, & Hein, 2010; Richard, Luck, & Hollingworth, 2008; Tas, Dodd, & Hollingworth, 2012) when establishing object continuity in dynamic environments.

In the context of transsaccadic updating, object-mediated updating process offers an explanation for why, under visual stability, participants are highly insensitive to spatial displacements of the target object (Bridgeman et al., 1975). As discussed above, if the pre- and post-saccadic properties of the target are similar, then the visual system will establish stability, and the saccade target will be perceived as continuous. The pre-saccadic representation of the target object will be updated with its final, post-saccadic properties. In the displacement detection experiments, this would result in overwriting of the pre-saccadic position of the target with its post-saccadic position in the no-blank trials. Due to this overwriting process, the visual system loses access to the precise pre-saccadic position, making it difficult for the participants to report the direction of spatial displacement. When the pre- and post-saccadic properties of the target object are sufficiently distinct, then visual stability will be disrupted, and correspondence will not be established. Blanking the target (Deubel et al., 1996); changing its surface features, such as shape (Demeyer et al., 2010a) or contrast polarity (Tas, Moore, et al., 2012); or changing the target's identity (Tas, Moore, et al., 2012) disrupts the target's continuity. In all of these situations, the pre- and post-saccadic properties are mapped to two distinct objects. As a result, the visual system can easily access and compare the locations of both pre- and post-saccadic objects, increasing the displacement detection accuracy.

The results of the displacement detection experiments clearly suggest that multiple features of the target object are encoded and used to establish object continuity across saccades. They also indirectly suggest that for conditions where visual stability is established, the precise feature information of the target object is inaccessible, possibly as a result of an object-mediated updating process. One limitation of these previous studies is that they assessed the updating of the pre-saccadic representation by asking participants to compare the pre- and post-saccadic properties of the target object, rather than directly assessing the pre-saccadic feature representation. For instance, instead of an automatic overwriting mechanism, as proposed by the object-mediated updating framework, the representational updating may be achieved with an integration mechanism in which the pre- and post-saccadic feature values are merged into a single representation. In both of these scenarios, the precise pre-saccadic feature value would be inaccessible, resulting in similar displacement detection performance. Therefore, in order to determine the underlying mechanisms of transsaccadic updating, we need to directly measure the properties of both the pre- and post-saccadic representations of the saccade target object. This way, it is possible to understand how pre- and post-saccadic representations of the same object are reconciled with the continuing representation of the target. The present dissertation was designed to directly test the mechanisms of transsaccadic updating under conditions of stability and instability.

Summary

In Chapter 1, I reviewed the accounts that explain how the visual system establishes object correspondence across saccades. The current evidence favors object-based accounts (Currie et al., 2000). According to this view, the visual system encodes the pre-saccadic information about the saccade target object and compares it with the post-saccadic information after the saccade lands. A match between these two representations will result in perception of stability while a mismatch would be perceived as disruption of stability. After this correspondence process, the visual system is left with multiple representations of the visual scene that are acquired during fixations. To perceive a unified visual world, the visual system must reconcile the peripheral (pre-saccadic) and foveal (post-saccadic) representations of the objects. It is unclear; however, how the visual system handles these separate representations of the same object. What are the mechanisms by which the visual system builds an integrated mental representation of the environment? Although the present work focusses on updating across the saccades, this updating mechanism is likely to be integral to any type of situation in which the visual system needs to establish object correspondence and maintain coherent representations of objects across time and change. Therefore, the present dissertation will also shed light to general mechanisms of representational updating that are used to reconcile any type of perceptual discontinuity.

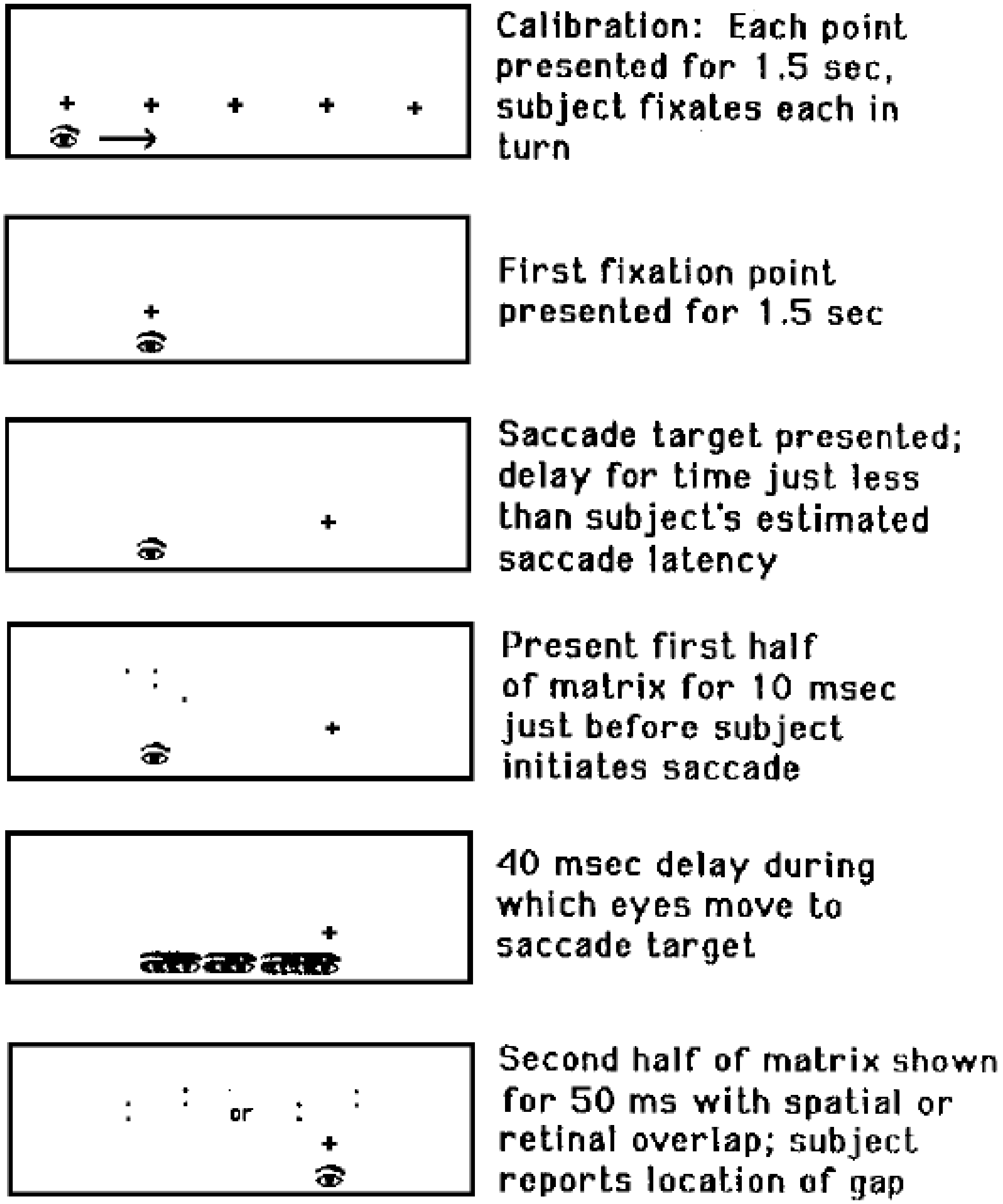

Figure 1.1. Events in a sample trial in Irwin et al. (1988). The eye figure indicates the location of participants’ gaze.

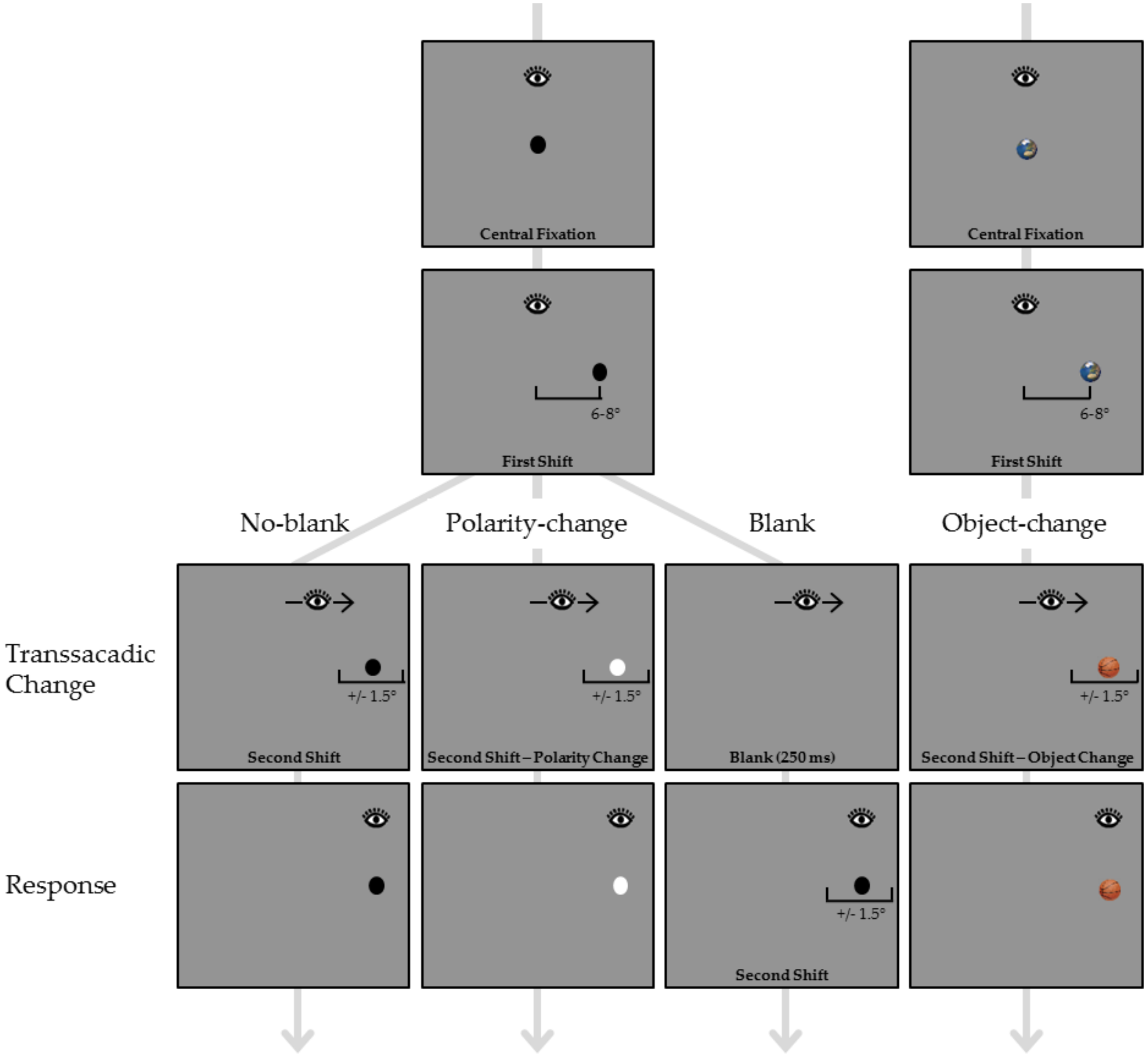

Figure 1.2. Intrasaccadic target displacement paradigm in the no-blank, polarity change, blank, and object-change conditions used in the experiments of Tas, Moore, et al. (2012). The stimuli are not drawn to scale.

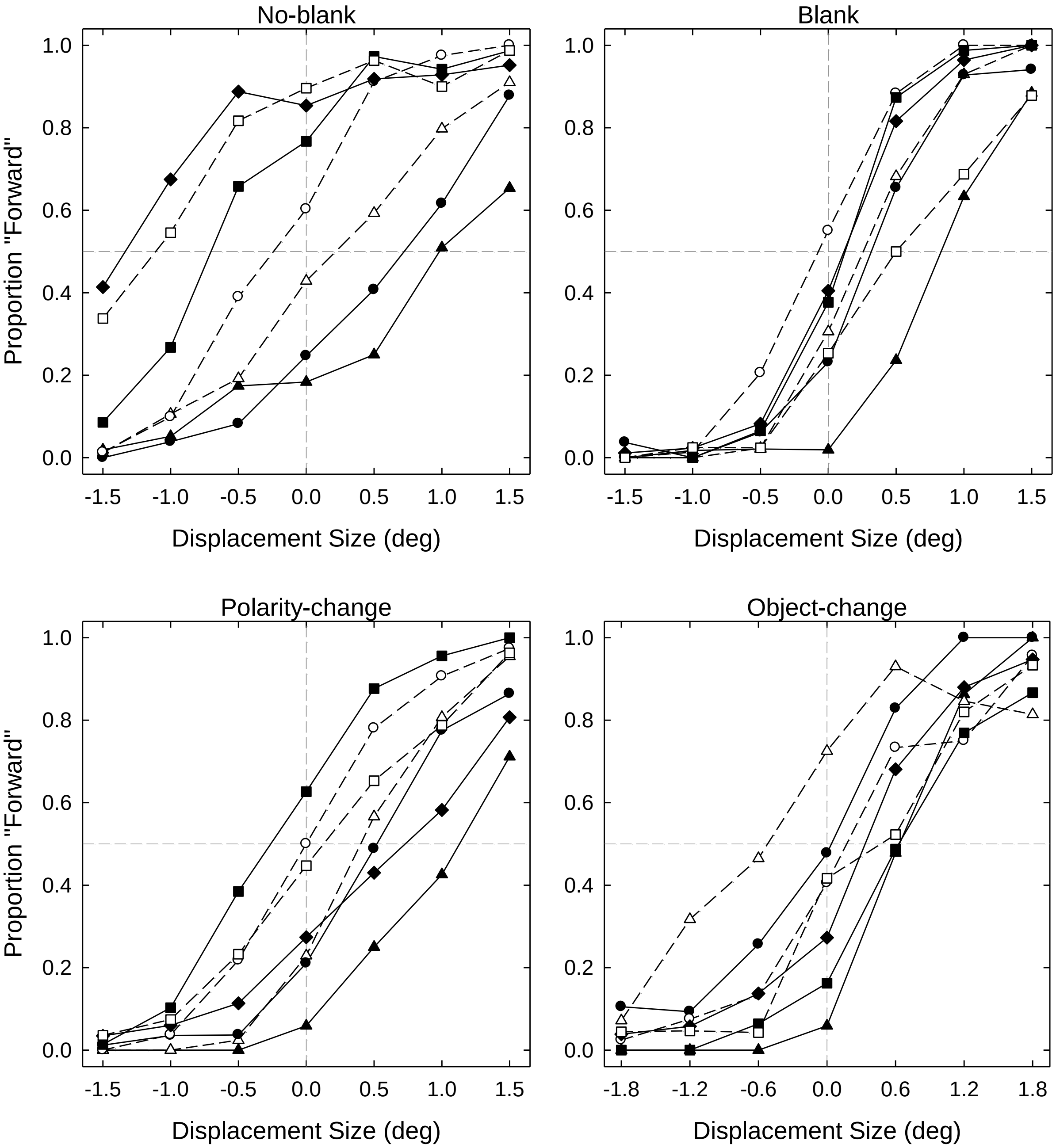

Figure 1.3. The results of Tas, Moore, et al. (2012)experiments. Proportion of forward responses was plotted as a function of displacement size. Each line represents one participant. Positive values indicate trials where the second shift was the same direction as the first shift. Negative values indicate trials where the second shift was to the opposite direction of the first shift.

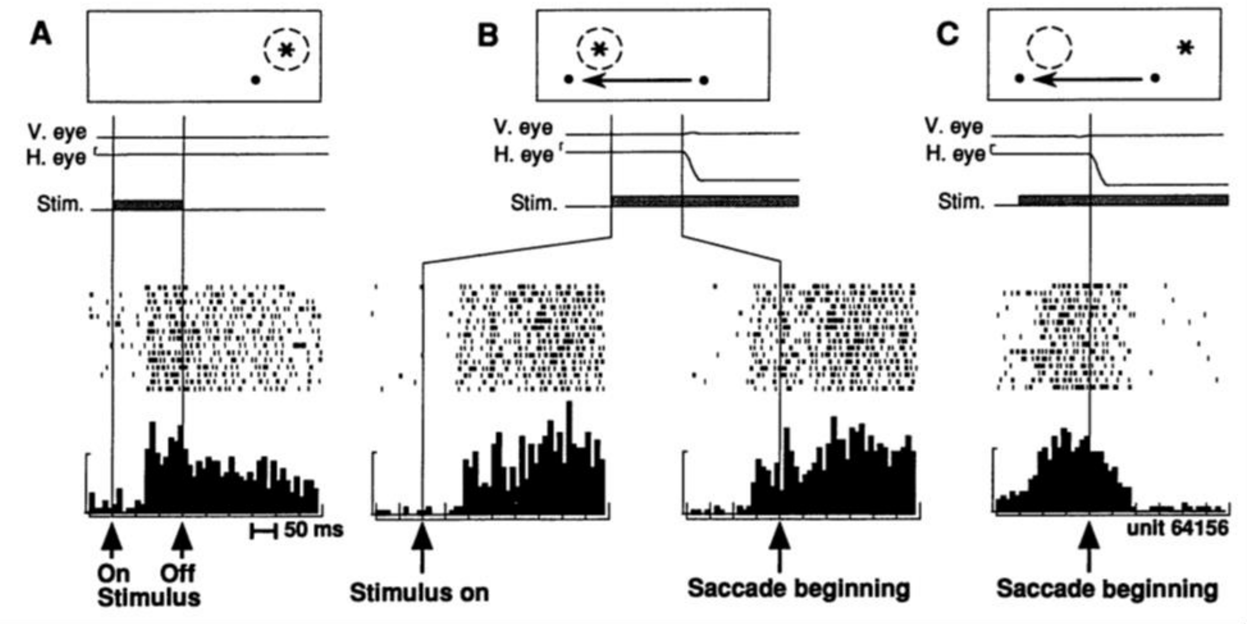

Figure 1.4. Results of Duhamel et al. (1992). Panel A: Activation of an LIP neuron for stimulus presented in its receptive field during a fixation task. Panel B: Responses to a stimulus in FF. Right panel is aligned on the execution of the saccade. Note that the neuronal responses began prior to actual saccade execution, a result used as evidence for predictive remapping. Panel C: Responses for a stimulus that is no longer in the RF as a result of a saccade execution. The neuron's response decreases sharply when a saccade removes the stimulus from the RF, compared to the persistent response even when the stimulus is turned off in Panel A.

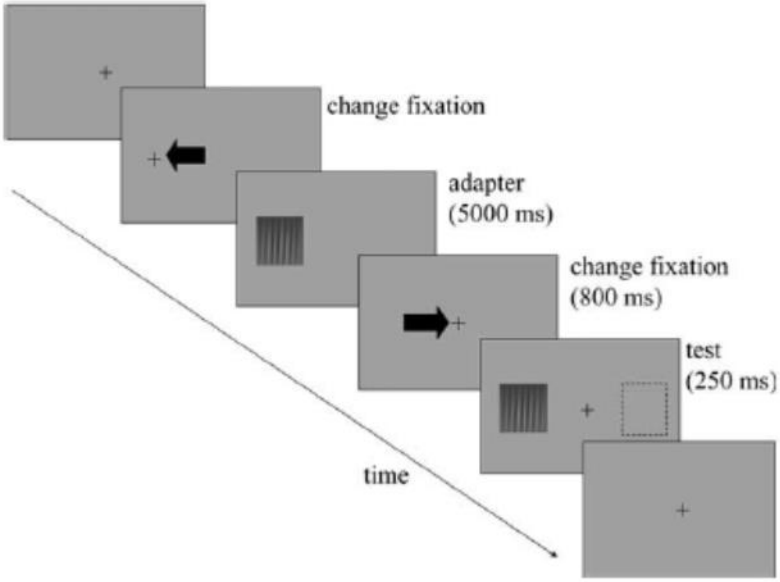

Figure 1.5. The sequence of events in the transsaccadic adaptation aftereffect experiments of Melcher (2005).

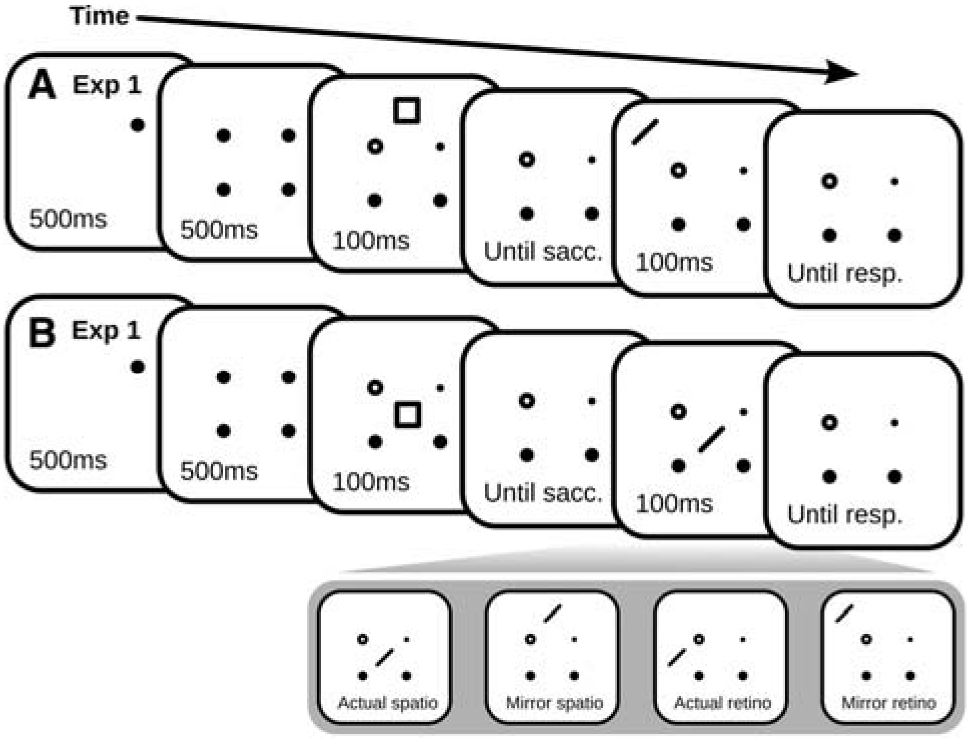

Figure 1.6. A sample trial in the retinotopic target location condition (Panel A) and in the spatiotopic target location condition (Panel B) in Experiment 1 of Mathôt and Theeuwes (2010a). In a typical trial, participants started fixating the gray dot which then followed by three additional dots. One of these three dots was cued by changing its color to green, informing participants to execute a saccade to it. In this example, the saccade target is presented as the open circle. Attention was cued with the abrupt-onset item (the square). The bottom panel in gray represents four possible target locations: spatiotopic, spatiotopic control, retinotopic, retinotopic control.

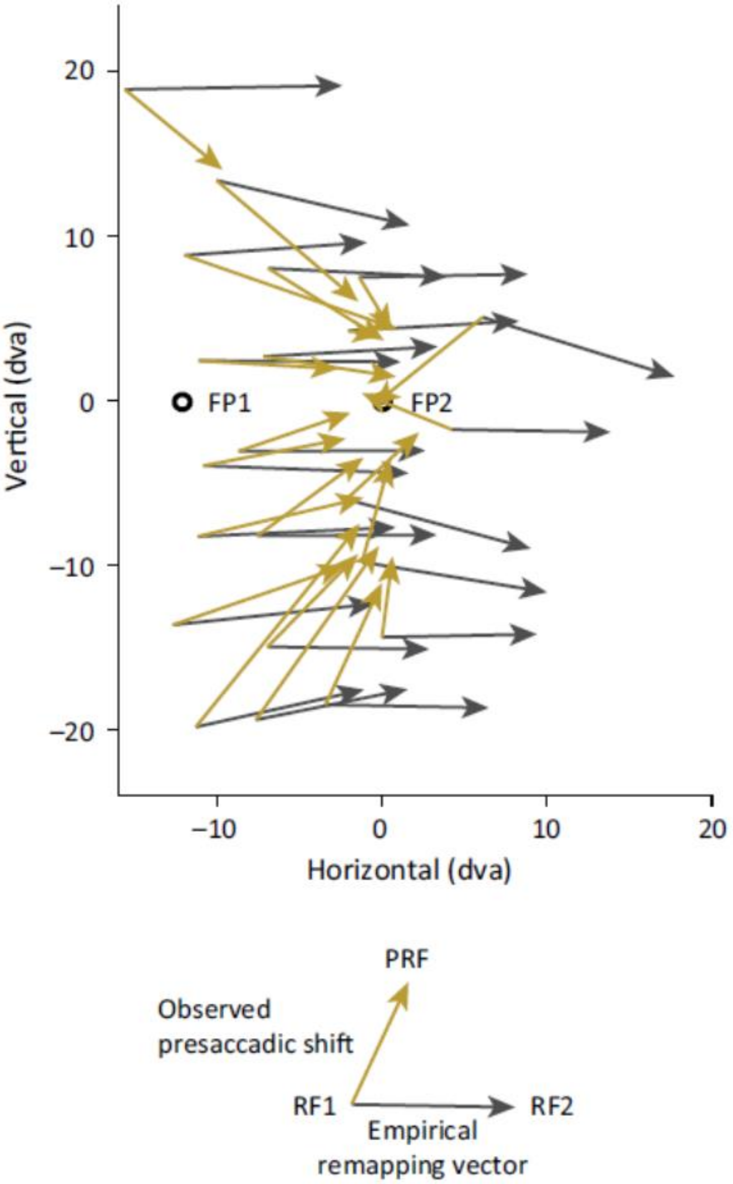

Figure 1.7. Neuronal evidence for convergence of RFs. Observed (gold vectors) and predicted remapped (black vectors) receptive field shifts of FEF neurons in Zirnsak et al. (2014) experiment after a saccade execution to a target at fixation point 2 (FP2). Note that the RFs actually converge toward the location of the saccade target.

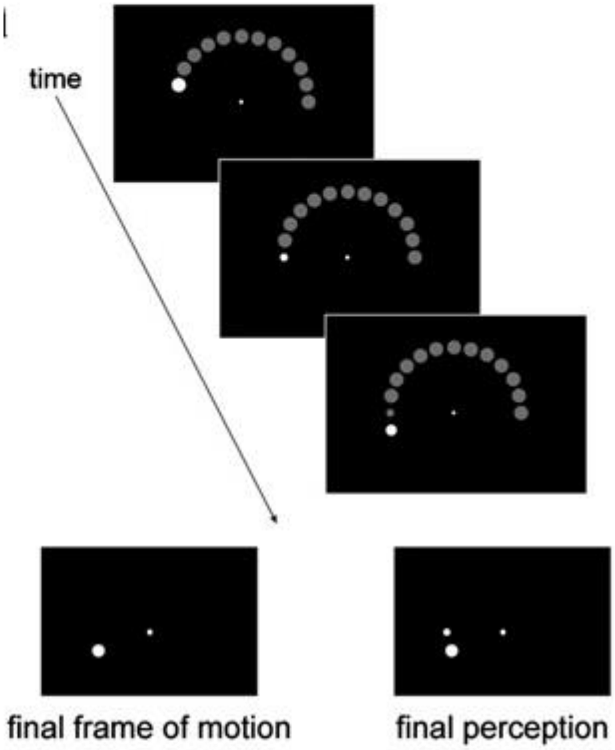

Figure 1.8. The stimuli used in C. M. Moore et al. (2007) and the final perception the stimuli in the size change condition. The gray disks show the path of the white disk during apparent motion. In this example, the disk's size was decreased at the second-to-last frame, disrupting object continuity. Participants frequently reported seeing two disks at the end of the sequence while in reality the final frame of motion contained a single object.

CHAPTER II

PRESENT STUDY

Aim

While exploring a scene, humans perceive the world as smooth and continuous. However, the input our visual system receives is constantly changing and sometimes even incomplete due to frequent motion of the eyes, head, and the body. Eye movements, particularly, create multiple problems for the visual system. First, information reaching to our visual system is not continuous. Saccadic eye movements leave the visual system with brief, high quality information, followed by fast movement of the eyes. Second, with every eye movement, the locations of objects on the retina shift. Third, saccades are often imprecise. They frequently fail to land on the target object (Becker, 1991). Finally, although the objects do not unexpectedly change locations or features as in laboratory experiments, their peripheral and foveal perceptions differ due to acuity differences across the retina (Herwig & Schneider, 2014; Land & Tatler, 2009). Despite all of these obstacles, the visual system can successfully create a continuous perception of the visual world.

As reviewed in Chapter 1, previous work determined that transsaccadic object correspondence is achieved with a process by which the pre- and post-saccadic representations of the target object are compared. At the end of this correspondence process, the visual system is left with two separate representations of the same object: pre-saccadic and post-saccadic. How, then, are these discrete representations incorporated into a persisting representation of an individual object? Although some studies investigated how pre-saccadic features affect perceptual judgments of the post-saccadic objects (e.g., Fracasso, Caramazza, & Melcher, 2010; Henderson & Siefert, 1999; Melcher, 2009; Wittenberg, Bremmer, & Wachtler, 2008), little is known about the specific mechanisms by which the pre- and post-saccadic features are incorporated to give us a perception of a continuous scene. How are the object representations updated after each saccade to reflect the newly perceived post-saccadic properties? Is this updating mechanism sensitive to pre-saccadic properties of the target, resulting in an interaction of the pre- and post-saccadic features, or does it only depend on the post-saccadic representation?

In the following section, I will first discuss the possible mechanisms by which object representations are updated to reflect the post-saccadic information, and the extent to which the pre-saccadic information interacts with the post-saccadic information. Then, I will explain the task I developed and how it can help us to differentiate these different hypotheses.

General Method and Hypotheses

In the following experiments, I investigated three possible mechanisms by which the pre- and post-saccadic information are related to each other: overwriting, feature integration, and multiple states. Overwriting and integration mechanisms assume that at the end of the updating process, there is only a single representation of the object. Therefore, the specific states of the object before the saccade (overwriting) or before and after the saccade (integration) are lost. In contrast, the multiple states mechanism holds that participants can successfully maintain multiple representations of different states of the same object.

The overwriting hypothesis was motivated from a strong version of the object-mediated updating framework (Enns et al., 2009; C. M. Moore & Enns, 2004; C. M. Moore et al., 2007). According to this framework, if visual stability is established, and the post-saccadic object is perceived as the continuation of the pre-saccadic object, the properties of the saccade target object are overwritten by the post-saccadic properties. This overwriting process renders the initial properties of the saccade target object inaccessible for report. Therefore, at the end of the saccade, there is only one representation of the object: the post-saccadic. Overwriting can, in fact, be a plausible mechanism of transsaccadic updating given that the post-saccadic information is more reliable than the pre-saccadic information, because it is based on foveal information, rather than on peripheral or parafoveal information. One of the principal goals of the following experiments was to determine if the transsaccadic updating mechanism leads to complete overwriting of the pre-saccadic properties, as suggested by this framework, and if the pre-saccadic feature information can be reported with high precision when visual stability is disrupted and object correspondence fails.

A second possibility is that the pre- and post-saccadic features are integrated into a composite representation. In this case, the visual system would lose the precise pre- and post-saccadic states of the object, and there will be a single representation at the end of the saccade, with the represented feature value being a mixture of the pre- and post-saccadic values. One's report of the pre- and post- saccadic features should be similar and should reflect an intermediate value.

In contrast to the overwriting and integration mechanisms, a third possibility assumes that visual system can maintain multiple states of the same object. It is often necessary to represent a single object as having existed in multiple different states (e.g., a face as having been angry but now happy). Thus, it is possible that the visual system retains more than one representation an individual object's features without disrupting object correspondence, even across the very rapid events that constitute transsaccadic perception. In this case, the visual system should be able to access to both states, if necessary. However, it is possible that these two discrete states might interact with each other in some subtle way. Different possible feature interactions are discussed below.

To test these different alternatives, in the main experiments of the dissertation, I used a continuous report task to measure the representations of the pre- and post-saccadic objects. The basic method was as follows (see Figure 2.1): Participants started by fixating the center of the screen. A small colored disk appeared either on the left or right side of fixation, and participants were instructed to execute a saccade to the disk. For half of the trials, the color of the disk remained the same throughout the trial. These no-color change trials were served as control condition, and were included to obtain a baseline level for color report and to measure any response biases participants may have. For the remaining half, the disk's color was changed to a new value during the saccade. Further, the magnitude of the color change was manipulated to test different sets of hypotheses. The results of Experiments 1 and 2 were used to determine the magnitude of color change which would not frequently disrupt visual stability. Participants' task was to report either the pre- or post-saccadic color value. At the end of each trial, participants were presented a color wheel, along with instructions about which color they need to report (pre- or post-saccadic). They made their responses by clicking on the appropriate color on the color wheel.

Earlier studies focused on either reports of the post-saccadic features, or asked participants to explicitly make a comparison decision. In the displacement detection studies described above, the inability to detect the target displacements when stability is established was interpreted as evidence that the visual system has a high tolerance for change when attempting to establish stability (Demeyer et al., 2010a; Deubel et al., 1996; MacKay, 1973; Mathôt & Theeuwes, 2011). According to this idea, the disruptions created by saccades are often considered as motor errors, because real-world objects usually do not change during the brief time that the eyes are in motion. This idea is plausible but does not illuminate how the pre- and post-saccadic representations of the target are reconciled. Tas, Moore, et al. (2012) suggested that the inability to access the pre-saccadic information is a result of an object-based overwriting mechanism; but, this process was inferred indirectly, without directly probing memory for the pre-saccadic location. It is certainly possible that the failure to detect position changes has a different cause. For example, if pre- and post-saccadic features were integrated, then the precise location of the pre-saccadic representation would be rendered less accessible, resulting in a poor performance in this comparison task. By using the continuous report task and asking participants to report the precise color of the pre- and post-saccadic representations, I was able to directly compare different possible mechanisms of object updating within the same experiment. It is important to emphasize that the present method generates similar memorial demands as the displacement detection task in which participants compare the pre- and post-saccadic locations. Specifically, both tasks require participants to encode the precise pre-saccadic property (location or color) in order to successfully complete the task. The main difference is whether the participants were asked to report the precise color, or to make a comparison judgment.

Because I propose that updating of the target depends on establishing object continuity across the saccade, I probed the representations of the pre- and post-saccadic stimuli either under conditions that were likely to generate the perception of a single, stable object or under conditions that were likely to generate instability and the perception of two objects. The primary method to induce instability was the blanking paradigm developed by Deubel and colleagues (1996). The experiments had two stability conditions: no-blank and blank. The no-blank condition was likely to lead to stability. In the blank condition, the target object was removed from the screen for 250 ms after the initiation of the saccade, leading participants fixating on an empty screen after the eyes landed (see Chapter 4 for details). In addition to the blanking manipulation, I used the degree of color change itself as a more fine-grained manipulation of stability. Color change magnitude was varied parametrically, with small color changes expected to generate a small proportion of trials on which object continuity was disrupted and large color changes expected to generate a larger proportion (Tas, Moore, et al., 2012). This allowed me to observe the differences in the pre- and post-saccadic representations as a function of a progressively greater probability that transsaccadic continuity was disrupted.

Figure 2.2 summarizes the predictions made by the object-mediated updating framework. For all the predictions, I focus the discussion on the main manipulation of stability, target blanking. In general, participants were expected to perceive one object under visual stability conditions (no-blank) and two objects when visual stability is disrupted (blank). First, consider trials in which the color of the disk remains the same throughout the trial (no-change, top row of Figure 2.2). Although the blank condition is predicted to lead to perception of two objects (pre- and post-saccadic disks), color report data would look exactly the same as in the no-blank condition because there is only one color to report. Thus, we cannot infer whether the participants' response is based on the pre-, the post-saccadic representation, or both. In this case, I expected to find accurate color responses for no-change trials, regardless of the stability manipulation: A single response distribution centered on the disk's color value.

Now consider the condition where the pre- and post-saccadic disks have different colors (color change, bottom row of Figure 2.2). First, for the blank trials where stability is disrupted, the pre- and post-saccadic disks should be represented as separate objects, leading to accurate reports of both colors. In this condition, I expected to find two separate distributions: One centered on the pre-saccadic color reflecting the trials in which participants are asked to report the pre-saccadic color and another centered on the post-saccadic color value reflecting the trials where participants report the post-saccadic color. For the no-blank trials, post-saccadic object should be represented as the continuation of the pre-saccadic object. The strong version of the object-mediated updating framework predicts that the pre-saccadic color will be overwritten by the post-saccadic color value, making the pre-saccadic color inaccessible. In this case, at the end of the saccade, only the post-saccadic representation should be accessible. Therefore, when asked to report the pre-saccadic color, participants should incorrectly report the post-saccadic value. If overwriting occurs in every trial, there would be a single distribution centered on the post-saccadic color value (bottom-left panel of Figure 2.2): Participants should report the post-saccadic value regardless of the color they were asked to report (i.e. pre-saccadic or post-saccadic). In addition to the prediction based on the blanking manipulation, I expected that the more fine-grained manipulation of color difference would lead to a range of probabilities that object continuity would be established. Thus, I expected that the frequency of overwriting would decrease as a function of increasing color difference, as depicted in Figure 2.3.

The second hypothesized mechanism is that, when continuity is established, pre- and post-saccadic features are integrated to form a composite representation. In contrast to overwriting, an integration hypothesis predicts that the pre- and post-saccadic distributions would be merged into one single response distribution (Figure 2.4A). The center of this combined distribution would depend on the relative weighting of the pre- and post-saccadic information. One might expect that, given the recency and higher precision of the post-saccadic, foveal representation, the merged value would lie closer to the post-saccadic value than to the pre-saccadic value.

Evidence for such merged perceptions comes from both visual working memory and masking literatures (Herzog & Koch, 2001; Johnson, Spencer, & Schöner, 2009; Suzuki & Cavanagh, 1998). Johnson et al. (2009) used a dynamic field model to capture performance in a change detection task. In a multi-item change-detection task where the model is presented with two colors to remember, they demonstrated a situation where the model incorrectly merges two colors into a single representation. This continuous updating occurred when the two colors are almost identical to each other. Since the smallest change between the pre- and post-saccadic colors in the following experiments was 30°, such a mechanism would need to be generalized to larger color differences. The fact that the two colors are mapped to the same object representation might facilitate integration at larger color differences. Further evidence for merged perceptions was reported by Herzog and Koch (2001). In their experiments, they presented participants with a target scene comprised of two tilted lines arranged vertically (Figure 2.5). The target was then followed by a grating mask which had two groups of three straight lines. Although perception of the target was successfully suppressed by the mask, its features were transferred (inherited) to the mask: Perception of the stimulus was a grating as the mask which was tilted as the target; that is, a merged representation of the target and the mask. Thus, there is clear evidence for merged feature values within a fixation. If similar integration were to occur across saccades, it would need to be functional over delays longer than the 30-50 ms delay used in Herzog and Koch. In addition, it would need to occur in spatiotopic rather retinotopic coordinates.

The final hypothesis concerns the possibility that, despite the presence of only a single object representation for the saccade target, multiple states of the object are preserved. If true, then the pre- and post-saccadic representations would have distinct response distributions. When asked to report the pre-saccadic value, participants should generate a response distribution at or near that value. When asked to report the post-saccadic value, participants should likewise generate a response distribution at or near that value. Although the distributions would be distinct, I considered the possibility that the two colors values interact with each other, causing the two distributions to deviate from the actual color values. The direction of this deviation might depend on the strength of the pre- and post-saccadic representations and the distance between the pre- and post-saccadic color values. For instance, if pre- and post-saccadic colors are close to each other, response distributions for the pre- and post-saccadic colors are expected to shift towards each other (Figure 2.4B). Alternatively, one of the colors may be represented more strongly than the other one, leading to attraction of the weakly represented color. In this case, one distribution would be centered on the correct color value and the other distribution would shift toward it (Figure 2.4C). This would be most plausible, for example, if a recent and precise foveal estimate of the post-saccadic value were to bias the representation of the less recent and less reliable peripheral representation of the pre-saccadic color. If, however, the distance between pre- and post-saccadic color values is far, then this interaction is expected to disappear, leading to accurate reports of both colors (Figure 2.4D). The following experiments were not designed to specifically compare these different shifting predictions. Therefore, with the current method it may be difficult to objectively quantify the magnitude of color change corresponding to “close” and “far” colors and their associated interactions. These multiple states predictions were tested by calculating the means of the response distributions and comparing them with the actual color value.

It should be noted that the single representation predictions and multiple states predictions may not be mutually exclusive. It is possible, for instance, to find 70% of the trials with overwriting and the remaining 30% of the trials with a shifted representation.

Such a result would suggest that even for the trials where the pre-saccadic color is not overwritten, its representation is affected by the post-saccadic color. Alternatively, it is possible to find 100% overwriting; leading to a single representation whose value is shifted toward the pre-saccadic value. Such a combination would suggest that the pre-saccadic information is not completely lost but affects the final perception of the object.

Evidence for shifted representations in visual working memory comes from a recent dynamic neural field model (Schneegans, Spencer, Schöner, Hwang, & Hollingworth, 2014). The model was developed to capture the relationship between visual working memory and saccade planning; therefore, its results can be taken as guidance for developing predictions for the current experiments. In one of their experiments, Schneegans et al. (2014) presented participants a single color to remember. During the retention interval, participants executed a saccade to a colored object. The color of this distractor object could be either similar or dissimilar to the memory target's color. Participants' color reports for the target color deviated toward the distractor color when the colors were similar but not when they were dissimilar.

Before making predictions based on their findings, it is important to consider the differences between their experiment and the current design. First, in their experiment the target and distractor objects were two separate objects, whereas in the current method, participants were asked to report either the pre- or post-saccadic color of the same target object. Second, the distance between the target and distractor colors was 20° in Schneegans et al.'s similar color condition. However, the smallest distance used in the following experiments was 30°. As mentioned above, "close" and "far" are relative terms, making it difficult to predict if two colors separated by 30° would have similar interactions as colors that are 20° apart. If these interactions in fact extend to larger color differences, it is possible to observe similar shifts in the following experiments.

Golomb, L'Heureux, and Kanwisher (2014) presented further evidence for shifted feature representations. In their experiments, participants were asked to report the color of a target square among distractor squares (Figure 2.6). The target location was cued at the beginning of the trial, and after the cue participants were instructed to execute a saccade before the colored squares appeared on the screen. Because the target color was presented only after the participants executed the saccade, their experiments did not directly test transsaccadic perception of the saccade target object. Instead, the authors focused on whether the representation of the target color was affected by a distractor color either at the retinotopic location or at the spatiotopic location. As in the current experiments, they used the continuous report task. The authors fitted the response distributions with mixture models, and showed that target reports were shifted toward the distractor color which was presented at the retinotopic location. As mentioned above, their study was not designed to test the representation of the saccade target. Similar deviations as in Schneegans et al. (2014) and Golomb et al. (2014) may be found in the following experiments, if the relationship between the two states of the same object is the same as the relationship between features of two different objects.

As discussed above, the color change magnitude was used as a secondary manipulation of visual stability. To determine the range of color change at which visual stability begins frequently being disrupted, in Chapter 3 I used the displacement detection task, and systematically manipulated the magnitude of color change between the pre- and post-saccadic states of the saccade target. Next, Chapter 4 discusses four main experiments in which I directly tested the predictions detailed in this chapter.

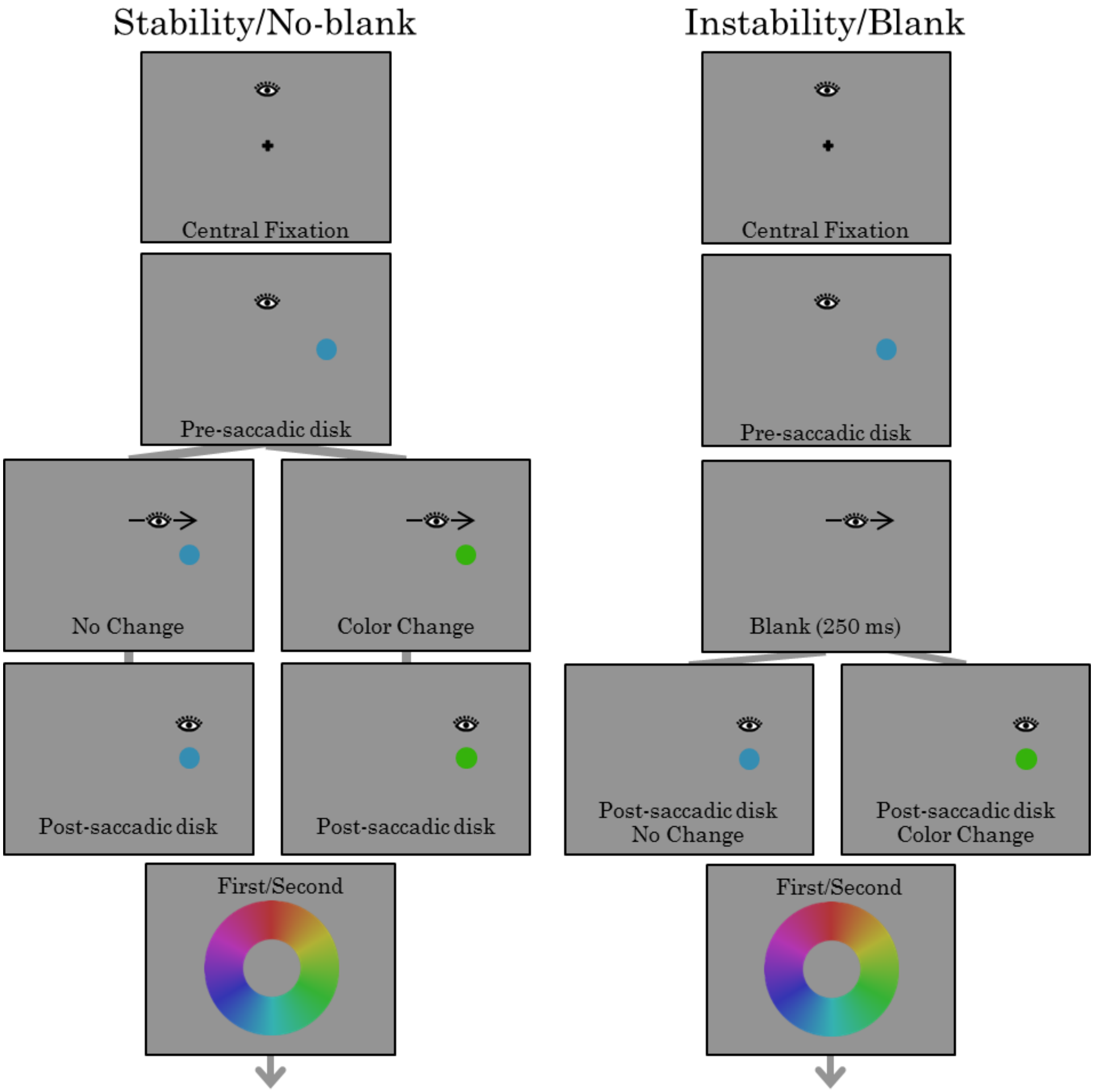

Figure 2.1. The sequence of events in Experiments 3-6. Left: No-blank (visual stability) condition, Right: Blank (visual instability condition). The stimuli are not drawn to scale. The eye icon represents participants' eye position for each step. The magnitude of color change in the example is 45°.

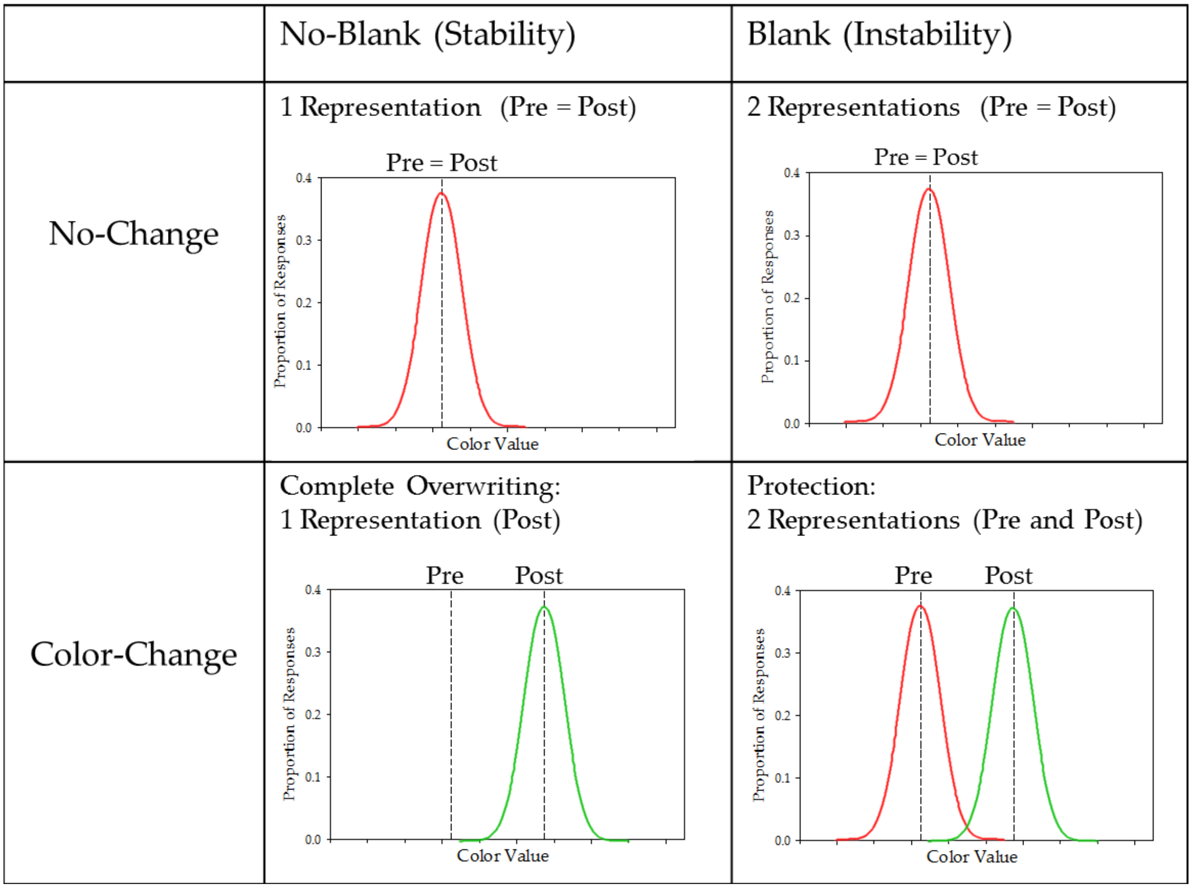

Figure 2.2. Predictions made by the strong object-mediated updating account. Hypothetical data show response frequency as a function of color value. The dashed lines represent hypothetical pre- and post-saccadic color values. For no-blank/color-change condition, the figure only shows hypothetical results in case of complete overwriting.

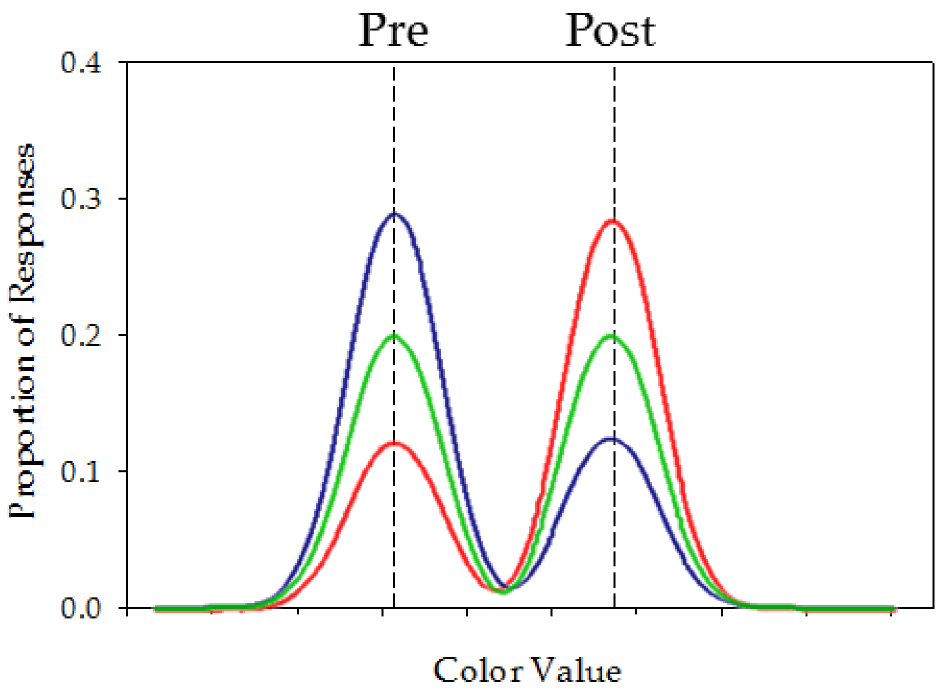

Figure 2.3. Hypothetical results for partial overwriting predictions. The proportion of responses is plotted as a function of color value. The dashed lines represent hypothetical pre- and post-saccadic color values. The colored lines represent the situations where overwriting occurs on 30%, 50%, or 70% of the trials, shown in blue, green, and red lines respectively. It is predicted that as the magnitude of color change increases, the proportion of trials in which overwriting is observed decreases due to disruptions created by color change alone.

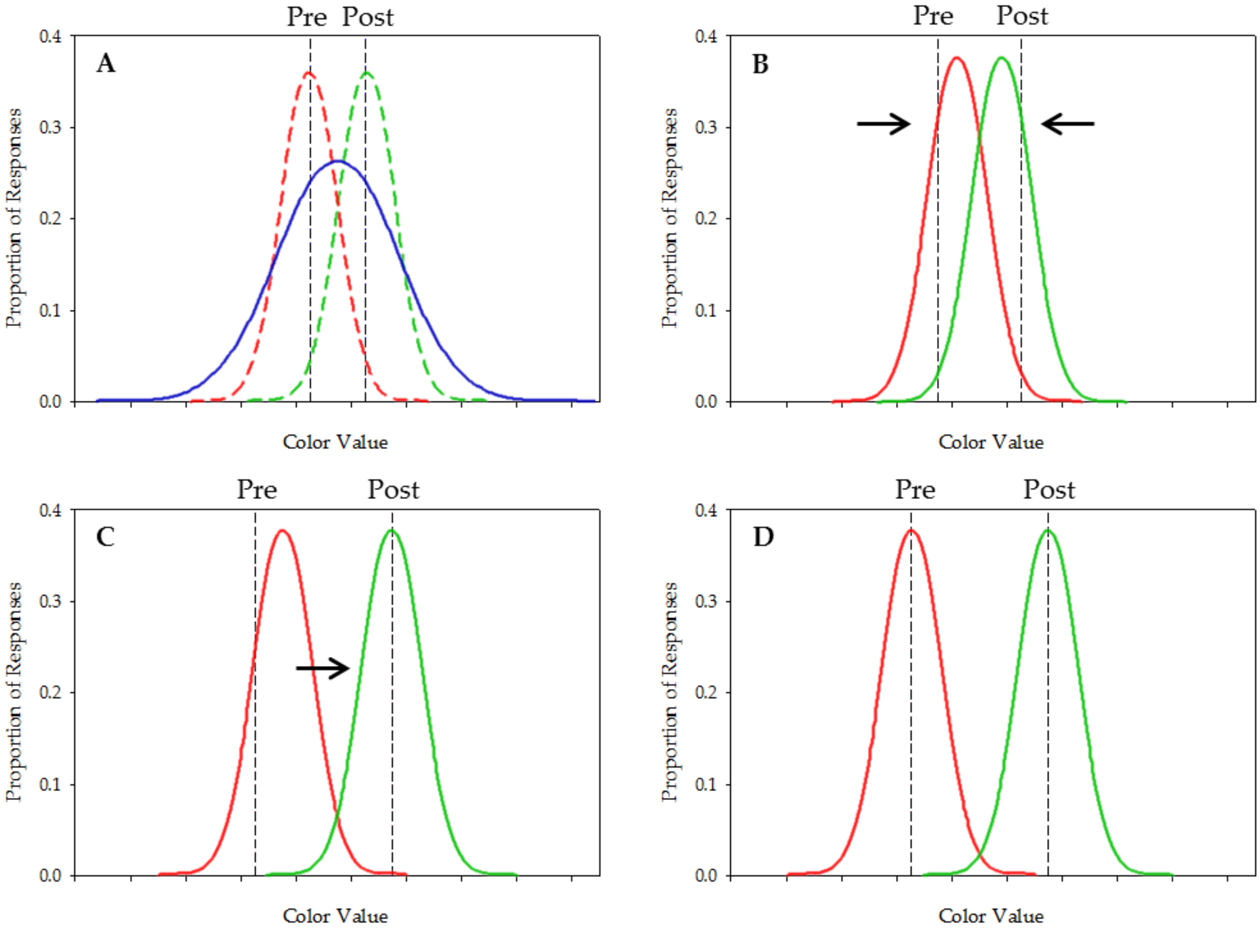

Figure 2.4. Hypothetical data for the integration and multiple states predictions. The dashed lines represent hypothetical color values for the pre- and post-saccadic disks. (A) Integrated representation. The dashed distributions represent separate hypothetical representations centered on the pre- and post-saccadic colors while the blue distribution is their hypothetical merged response distribution. (B & C) Shifted representations. (D) Separate representations.

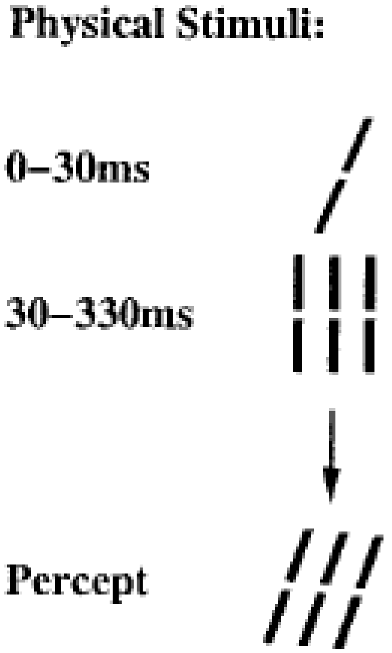

Figure 2.5. Stimuli and percept as reported in Herzog and Koch (2001). Target (top), mask (middle), and participants' percept (bottom).

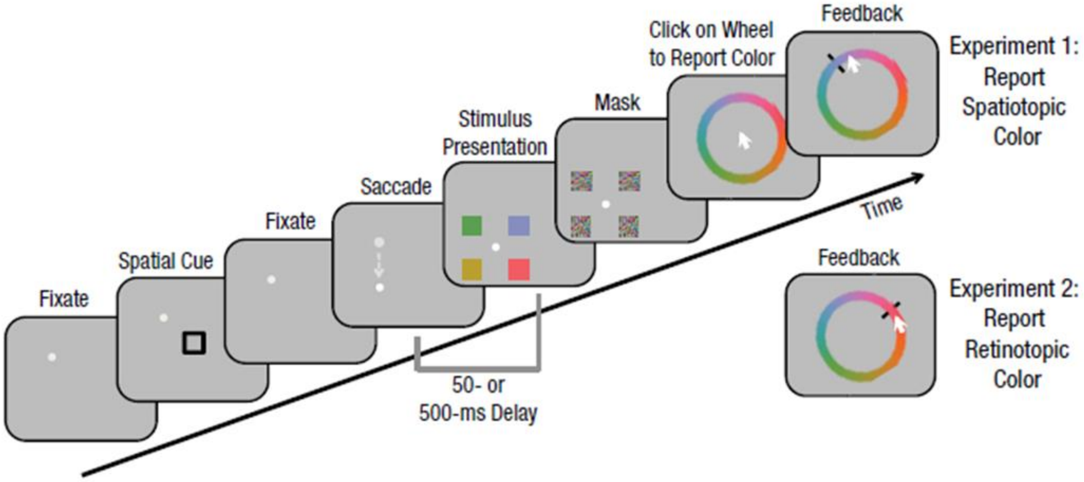

Figure 2.6. Sequence of events in a sample trial used in Experiments 1 and 2 of Golomb et al. (2014).

CHAPTER III

THE ROLE OF COLOR IN TRANSSACCADIC STABILITY

On the one hand, recent studies have shown that large surface feature changes between pre-and post-saccadic objects results in disruption of visual stability (Demeyer et al., 2010a; Tas, Moore, et al., 2012). On the other hand, the predictions regarding the fate of a saccade target's representation depend on whether visual stability is established. Thus, it is important to choose a range of color change in which the smallest values of change do not introduce a major disruption of stability on no-blank trials. Further, some of the hypotheses discussed above predict bimodality of the response distribution. To test these various predictions, the smallest color separation needed to be large enough to be able to detect two distinct distributions. To determine the maximum amount of color change which would not disrupt stability on a majority of trials, I ran two displacement detection experiments in which the magnitude of color change was systematically manipulated. In Experiments 1A and 1B, participants were asked to saccade to a peripheral colored disk. During the saccade, the spatial position of the disk was shifted either toward or away from the fixation. Participants' task was to report the direction of the spatial displacement. In addition to the spatial displacement, on some trials the color of the saccade target was changed to a new value. The magnitude of the color change was manipulated to determine the threshold when color change starts to induce visual instability. Perception of visual instability was assumed when displacement direction reports were significantly more accurate than in the control condition (no-color-change) (Demeyer et al., 2010a; Deubel et al., 1996; Tas, Moore, et al., 2012).

After determining the degree of color change that significantly increases displacement detection performance compared to the no-change condition, I tested whether color change disrupts stability to the same degree as the target blanking which will be the major source of instability in the main experiments. In Experiments 2A and 2B, the displacement detection task was combined with the target blanking method. As reviewed above, this type of target blanking has been shown to dramatically increase the perception of instability (e.g., Deubel et al., 1996). It is important to ensure that in the main experiments, visual stability is established on most of the color change trials so that target blanking is the main manipulation of stability. Experiments 2A and 2B were run to provide evidence that any disruption created by color change was less substantial than disruptions created by target blanking.

Experiment 1A

In Experiment 1A, participants were instructed to saccade to a colored target disk. During the saccade the color of the target was changed to a new value and the magnitude of color change between the pre- and post-saccadic disks was manipulated.

The intrasaccadic displacement detection task was used to measure perception of visual stability.

Method

Participants. Nineteen participants from the University of Iowa community (age range: 18-30; 11 male, 8 female) participated in Experiment 1A in exchange of either monetary compensation or course credit[2]. All reported normal or corrected-to normal vision and no color blindness. Three participants were eliminated from the analyses due to eye calibration problems. Two participants' data were eliminated due to technical problems with the eyetracker. The final analyses contained fourteen participants (9 male, 5 female).

Stimuli. All stimuli were presented on a neutral grey background. Pre- and post-saccadic objects were colored disks which subtended 0.68° of visual angle. The pre-saccadic disk's color value was randomly chosen at the beginning of each trial from a set of 360 possible colors equally distributed in HSV color space, with saturation and value (lightness) dimensions held constant at 0.7. In the baseline block (see below), the color of the post-saccadic disk always matched the color of the pre-saccadic disk. In the

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[2] Required sample size was determined with the help of MorePower 6.0.1 program (Campbell & Thompson, 2012). For Experiments 1A and 1B, I used a repeated measures design with 5 (Experiment 1A) and 6 (Experiment 1B) conditions. The results indicated that a minimum of 14 participants for Experiment 1A and 12 participants for Experiment 1B is needed to achieve a power level of .90 with an effect size (η^2) of .26.

experimental block, the color of the post-saccadic disk could either be the same as the pre-saccadic disk, or it could be changed by 15°, 30°, 45°, or 60° in color space. The change could be clockwise (CW) or counterclockwise (CCW).

Apparatus. In all of the following experiments, stimuli were displayed on a 17-in CRT monitor with a refresh rate of 100 Hz. The position of the right eye was monitored by an SR Research Eyelink 1000 video-based eye tracker sampling at 1000 Hz. A chin and forehead rest was used to ensure a viewing distance of 70 cm and to minimize movement of the head. Stimulus presentation was controlled with E-prime software (Schneider, Eschmann, & Zuccolotto, 2002).

Procedure. The experiment consisted of two blocks: baseline and experimental. The baseline block was used to determine the optimal magnitude of intrasaccadic position displacement which would lead to 70% accuracy in the standard displacement detection task for each subject. This displacement size was then used as the initial displacement size in the experimental block. The experimental block tested the effect of color change on visual stability.

The sequence of events for a typical trial is depicted in Figure 3.1. Each trial started with a black fixation cross at the center of the screen, and participants were instructed to fixate on the cross. After a variable interval of 1000-1500 ms, a colored disk appeared randomly either at the left or right side of the screen (pre-saccadic object).

Eccentricity of this pre-saccadic disk was chosen randomly within a range of 5°-7°. Participants were instructed to execute a saccade to the disk as quickly as possible. In half of the trials, the disk was shifted toward the center of the screen. In the remaining trials, it was shifted away from the center. This displacement occurred when the eyetracker detected that the eye crossed a 1.5° boundary from the center of the screen. After the completion of the saccade, the displaced disk (post-saccadic object) remained on the screen until participants made a displacement direction response. Participants were instructed to report the direction of the displacement in relation to the fixation cross (toward or away). For instance, if the disk appeared on the right side of the screen and then shifted to the left, the correct response would be toward. Participants made their responses via a serial button press box, with the buttons oriented vertically to eliminate any spatial response bias.

In the baseline block, the disk's color remained the same across the saccade and displacement. The magnitude of the spatial displacement was adjusted based on individual participant performance. This adjustment was done for two reasons. First, displacement detection task results in large performance variations. Thus, it is difficult to find a single displacement value which would yield similar accuracy levels across all participants. For instance, in the no-blank condition of Experiment 1 in Tas et al.'s (2012) study (see Figure 1.3), individual accuracy levels greatly varied for +0.5° displacements (from 20% correct to 100% correct). Second, using the same displacement value throughout the experiment can lead to saccadic adaptation where the motor system adjusts the amplitude of the saccade for predictable changes, leading the eyes to incorrectly land on the displaced target (McLaughlin, 1967). This motor correction can also affect perceptual judgments in target localizations (Bahcall & Kowler, 1999; Moidell & Bedell, 1988). A threshold of 70% correct displacement detection performance was used to encourage participants during the experiment. Decreasing this level may increase the number of mere guessing responses, and reduce participants' motivation. The 70% threshold chosen here should allow participants to see the displacement on most trials but nevertheless prevent ceiling effects.

The starting value for the displacement was 0.5° of visual angle. Displacement magnitude was adjusted using the transformed up-down procedure of Brown (1996) for a target accuracy of 70% correct. The displacement value was increased 0.1° after each incorrect trial and was decreased by 0.1° after two consecutive correct trials. The minimum displacement was set to 0.2°, and there was no upper limit for displacement value. The final displacement value in the baseline block was taken as the starting value in the experimental block.

In the experimental block, the main manipulation was the magnitude of color change. The sequence of events and the task were the same as in the baseline block.

However, the color of the disk could either remain the same throughout the trial, as in the baseline block, or it could be changed by 15°, 30°, 45°, or 60° (CW or CCW) during the saccade. The color change occurred at the same time as the spatial displacement. As in the baseline block, participants' accuracy for the 0° color change trials (*control condition*) was used to adjust displacement magnitude with the help of the transformed up-down method.

Participants first completed 40 baseline trials. Then, they completed a total of 400 experimental trials, 80 trials in each of the five color change conditions. The experimental trials were intermixed.

<u>Data Analysis.</u> In all of the experiments, saccades were defined with a combined threshold for velocity (>30°/s) and acceleration ($>9500°/s^2$). Trials in which participants did not maintain fixation at the fixation cross at the beginning of the trial (1% of the trials) and trials in which participants executed a saccade before the intrasaccadic position displacement occurred (<1% of the trials) were eliminated. I also eliminated trials in which saccade latency to the disk was less than 100 ms (1% of the trials) or longer than 2.5 standard deviation above the sample mean (> 690 ms, 2% of the trials). In the end, 5% of the trials were excluded from the analyses.

Results

Figure 3.2 shows mean accuracy as a function of color change. The displacement adjustment method led to a mean accuracy of 0.72 in the baseline block. Mean displacement sizes in the baseline and in the experimental blocks were 0.57° (min = 0.34°, max = 0.90°) and 0.52° (min = 0.33°, max = 0.79°) of visual angle, respectively. The direction of color change (CW or CCW) did not affect the pattern of results (all *p*s >.05) so the analyses reported here were run on collapsed data. To test the role of color change in visual stability in the experimental block, a one-way repeated-measures ANOVA was run with five levels of color change magnitude. The ANOVA revealed no significant effect of color change, $F(4, 52) = 1.53$, $p = .21$. Bonferroni corrected pairwise comparisons between the control condition and color change conditions of the experimental block showed no significant increase in displacement direction performance for any of the color change conditions.

The results of Experiment 1A suggest that color changes up to 60° do not significantly disrupt visual stability. In Experiment 1B, the magnitude of color change between the pre- and post-saccadic disks was increased to determine the color change range where visual stability is frequently disrupted.

Experiment 1B

In Experiment 1A, none of the color change conditions differed significantly from the control condition. I increased the maximum magnitude of color change to 90° in Experiment 1B to find the value at which displacement detection performance significantly increases compared to the control condition. The method of Experiment 1B was the same as Experiment 1A, except for the differences noted below.

Method

Participants. Twenty-five new participants (age range: 18-30; 12 male, 13 female) from the University of Iowa community participated in Experiment 1B in exchange of course credit. All reported normal or corrected-to normal vision and none of them reported color blindness. Data from three participants (1 male, 2 female) were eliminated from the analyses due to problems with eye calibration, an additional participant (male) was eliminated from the analyses because of failure to comply with the instructions (i.e., used the wrong buttons for responses throughout the experiment). Therefore, the following analyses included 21 participants (10 male, 11 female).

Stimuli. The stimuli were the same as Experiment 1A, except that the magnitude of color change between pre- and post-saccadic disks could be 0° (control condition), 30°, 45°, 60°, 75°, or 90°.

Procedure. In Experiment 1A, performance never reached at ceiling level as the magnitude of color change increased. The largest increase in individual participant performance between 0° and 60° color changes was only 13%. In Experiment 1B, the same displacement size adjustment was implemented but this time the up-down procedure was modified to achieve a mean accuracy of approximately 60%. Lowering the accuracy in the control condition should allow more room for participants to improve their accuracy. The method for adjusting the displacement size was as follows (Brown, 1996): As in Experiment 1A, the initial displacement size was 0.5° for each participant. This time, however, the trial counter tracked up to three consecutive trials. The counter was reset every time a rule was implemented. If the first trial was incorrect, the displacement value was increased for 0.1°. If the first trial was correct, the counter waited for the second trial. If the second trial was also correct (correct-correct), the value was decreased for 0.1°. An incorrect second trial led the counter to make a decision based on the third consecutive trial. After a correct-incorrect-correct sequence, the value was decreased for 0.1° while a correct-incorrect-incorrect sequence led to increasing of the value for 0.1°. As in Experiment 1A, there was no maximum size of displacement, but the minimum size could not be less than 0.2°.

Participants completed 40 trials in the baseline block and 70 trials in each of six change conditions, leading to a total of 460 trials.

Results

Trials were eliminated if the participant did not maintain fixation at the beginning of the trial (2% of trials), if a saccade was executed before the position displacement occurred (<1% of trials), and if the saccade latency to the disk was shorter than 100 ms (2% of trials) or longer than 2.5 standard deviation (670 ms, 2% of trials). A total of 6% of the trials was excluded from the analyses.

The results are depicted in Figure 3.3. Displacement detection performance in the baseline block was 0.65. Mean displacement size in the baseline block was 0.49° of visual angle (min = 0.25°, max = 1.49°), and mean displacement size in the experimental block was 0.38° of visual angle (min = 0.24°, max = 0.83°). The direction of change (CW or CCW) did not affect the pattern of results, so data were collapsed for the analyses (all *p*s > .05). A repeated measures of ANOVA revealed a significant effect of color change magnitude, *F*(5, 100) = 5.84, *p* < .001. Bonferroni corrected pairwise comparisons showed that performance did not significantly improve for the 30° and 45° color change conditions relative to the control, condition, *t*(20) = -1.66, *p* = .11 and *t*(20) = -1.31, *p* = .21, respectively. However, for 60°, 75°, and 90° color change conditions, detection performance significantly increased compared to the control condition, *t*(20) = -2.98, *p* = .007, *t*(20) = -3.6, *p* = .002, and *t*(20) = -3.34, *p* = .003, respectively. Together with the results of Experiment 1A, these findings suggest that disruptions created by the color change becomes significantly more frequent when the color change between the pre- and post-saccadic objects is 60° or greater.

Experiments 2A and 2B

In the main experiments, I used the intrasaccadic target blanking paradigm as the main manipulation of object continuity. The aim of Experiments 2A and 2B were to confirm that even though a color change can disrupt visual stability in some trials, its effect is minor compared to the disruption created by target blanking. Previously, we have shown that multiple surface feature changes are required to produce an effect that is similar in magnitude of that created by target blanking (Tas, Moore, et al., 2012). In Experiments 2A and 2B, blanking and color change were crossed to test the relative contributions of feature and object discontinuity in disrupting visual stability. The method and the task were the same as in Experiments 1A and 1B, except that for half of the trials the saccade target was blanked. In Experiment 2A, the magnitude of color change was 45°, in Experiment 2B it was 60°. In line with previous findings (Tas, Moore, et al., 2012), I predicted that displacement detection responses will be significantly more accurate in the blank than in the color change trials.

Method

Participants. Eighteen (age range: 18-30; 6 male, 12 female) and nineteen (age range: 18-30; 6 male, 13 female) new participants completed Experiment 2A and Experiment 2B, respectively. All participants were given course credit as compensation. All reported normal or corrected-to-normal vision. At the beginning of the experiment, each participant was screened for color blindness with the 14-plate version of Ishihara color blindness test. Data from four participants in Experiment 2A (2 male, 2 female) and four participants in Experiment 2B (1 male, 3 female) were excluded from the analyses due to problems with eye calibration. Data from an additional participant (female) were excluded in Experiment 2B due to participant not complying with the instructions (i.e. chance level performance throughout the experiment) resulting in 14 participants in each experiment.[3]

Stimuli. The stimuli were the same as used in Experiments 1A and 1B, except that for the color-change trials, the magnitude of color change between pre- and post-saccadic disks was always 45° in Experiment 2A and 60° in Experiment 2B.

Procedure. The procedure was exactly the same in both Experiments 2A and 2B. The design was a 2 (Target Blanking: No-Blank, Blank) x 2 (Color Change: No-Change, Change) within-subjects design. The no-blank trials were implemented in the same manner as in Experiments 1A and 1B. For blank trials, the target object was removed from the screen for 250 ms when the tracker detected that the eye crossed a boundary of 2° from the central fixation. After the blank, the target was presented at its displaced

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[3] Sample size analyses revealed that a minimum of 14 participants is needed to achieve a power level of .90 with an effect size (η^2) of .50 for a 2x2 design experiment. The effect size in these analyses was taken from the analyses Tas et al. (2012, Experiment 2) which used a similar design.

location. For trials where both a blank and a color-change occurred, the target was presented at the displaced location in a new color. The magnitude of color change between the pre- and post-saccadic disks was 45° in Experiment 2A and 60° in Experiment 2B. For half the trials, the direction of the change was clockwise. For the remaining half, it was counterclockwise. At the end of each trial, the disk stayed on the screen until the participant made a response.

Participants first completed a baseline block where only no-blank/no-change trials were presented. Performance in the baseline condition was tracked and manipulated to obtain a mean accuracy of approximately 65% which was the mean accuracy level in the baseline block of Experiment 1B. The method of adjustment was to increase the displacement size for sequences of 'incorrect-incorrect', 'correct-incorrect', or 'correct-correct-incorrect' trials, and to decrease for trial sequences of 'incorrect-correct' or 'correct-correct-correct'(Brown, 1996). The initial displacement size was 0.6° for each participant.

The magnitude of the size adjustment was also manipulated throughout the baseline block. That is, the adjustment size was 0.1° for the first 20 trials, 0.06° for the next 20 trials, and 0.02° for the last 20 trials. Systematically decreasing the adjustment size was done to stabilize the magnitude of change toward the end of the baseline block. The method for the size adjustment during the experimental block was also changed.

As in the previous experiments, only responses in 0° color change trials were tracked. However, this time performance was recorded for 10 trials. If average detection accuracy was below 60%, the size was increased by 0.04°. For 60% or 70% accuracy, the size was increased by 0.02° and decreased by 0.02°, respectively. For 80% of accuracy, the size was decreased by 0.06°, and lastly if detection performance was above 80%, the size was decreased by 0.1° of visual angle. The reason for this type of accuracy-dependent scaling was to acquire a mean accuracy level of 65% without the need of manipulating the displacement size too frequently, as well as eliminating large fluctuations of displacement magnitude.

In both Experiments 2A and 2B, participants first completed 60 trials in the baseline block followed by 110 trials in each of four conditions, leading to a total of 500 trials. Trial type was mixed in the experimental block.

Results

Trials on which participants did not maintain fixation at the beginning of the trial (3% in Experiment 2A and 2% in Experiment 2B), trials on which participants executed a saccade before the position displacement occurred in the no-blank trials (2% in Experiment 2A and <1% in Experiment 2B), and trials on which the saccade latency to the disk was shorter than 100 ms (2% in both Experiments 2A and 2B) or longer than 2.5 standard deviations (850 ms, 2% in Experiment 2A and 910 ms, 2% in Experiment 2B) were eliminated. In the end, 9% of the trials in Experiment 2A and 6% of the trials in Experiment 2B were excluded from the analyses.

Figures 3.4 and 3.5 display the results of Experiment 2A and 2B, respectively. The adjustment method yielded mean accuracy levels of 0.73 in Experiment 2A and 0.69 in Experiment 2B. Mean displacement size in the baseline block was 0.46° of visual angle (min = 0.28°, max = 0.95°) in Experiment 2A and 0.46° (min = 0.29°, max = 0.79°) in Experiment 2B. In the experimental block, it was 0.34° of visual angle (min = 0.16°, max = 0.74°) in Experiment 2A and 0.33° (min = 0.17°, max = 0.60°) in Experiment 2B. The direction of change (CW or CCW) did not influence the pattern of results in neither Experiment 2A nor in 2B, so trials were collapsed for the analyses (all *p*s > .05).

First, a 2 x 2 repeated measures of ANOVA showed a significant main effect of target blanking in both Experiments 2A and 2B, $F(1,13) = 67.27$, $p < .001$ and $F(1,13) = 79.54$, $p < .001$, respectively. Replicating the results of Experiments 1A and 1B, the main effect of color change was not significant for 45° color changes but approached significance for 60° color changes, $F < 1$ and $F(1,13) = 4.39$, $p = .06$, respectively. Blank x color change interactions were significant in both Experiments 2A and 2B, $F(1,13) = 5.68$, $p = .033$ and $F(1,13) = 22.41$, $p < .001$, respectively. The significant interactions were driven by a difference in the influence of color change on no-blank and blank trials. In both experiments, the effect of color change was larger in the no-blank than in the blank condition, although this effect reached significance in Experiment 2B, *t*(13) = -4.31, *p* = .001, but not in Experiment 2A, *t*(13) = -1.69, *p* = .11. For the blank condition, color change did not significantly affect displacement detection performance, *t* < 1 and *t*(13) = 0.97, *p* = .35, in Experiments 2A and 2B respectively.

To summarize, the results of Experiments 2A and 2B showed that (1) blanking the saccade-target object results in significant disruption of visual stability; (2) color change creates significantly more frequent disruptions of visual stability if its magnitude is approximately 60° or more; and (3) the effect of blanking on visual stability is stronger than color changes as large as 60°; (4) blanking the target object maximally disrupts object continuity, thus additional changes made to the object, like changing its color, does not further improve performance.

Discussion

The aim of Experiments 1 and 2 was to find the maximum magnitude of color change that will not induce visual instability on most of the trials. Across four experiments, I found that visual stability is more likely to be disrupted if the color values of the pre- and post-saccadic objects are separated by approximately 60° or more on the color wheel. However, this finding does not suggest that color changes less than 60° never produce visual instability. For instance, in all experiments, 45° of color change resulted in numerically higher accuracy levels than no-change trials even though they were not significantly different from each other. Thus, 45° of color change might increase the probability of disrupting visual stability, but this increase indicates that the color changes up to 45° have minimal effects on the probability of disrupting stability, especially compared with the effect of target blanking.

In fact, the results of Experiments 2A and 3B showed that blanking the target object leads to significantly improved performance in a displacement detection task compared to 45° and 60° of color changes, indicating that the discontinuity created by target blanking is significantly stronger than by the discontinuity created by color changes up to 60° alone. In fact, the results of Experiments 2A and 2B suggest that blanking the target object maximally disrupts its continuity.

In the following experiments, in order to test all possible hypotheses discussed in Chapter 2, I used four different magnitudes of color change: 30°, 45°, 60°, and 75°. In light of these results, I can be confident that on most trials, 30° and 45° of color change will not result in object discontinuity. Although 60° and 75° of color change will result in some trials in which stability is disrupted by the color change alone, the blanking manipulation will be the major source of object discontinuity. Nevertheless, in the following experiments, caution was taken to interpret the data for changes of 60° and 75°, and the results were presented separately for these two magnitudes when necessary.

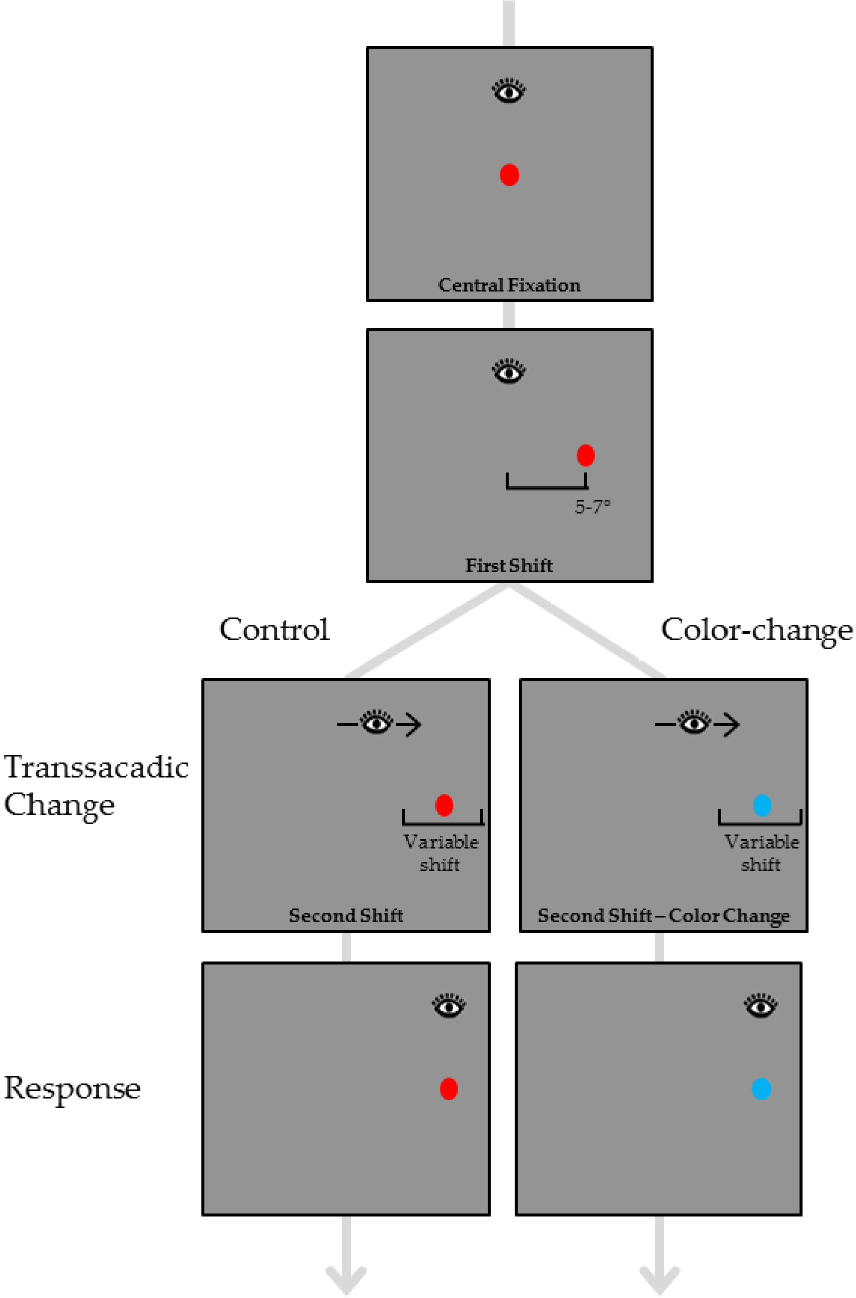

Figure 3.1. The sequence of events for the control (no-change) and color-change conditions used in Experiments 1A and 1B.

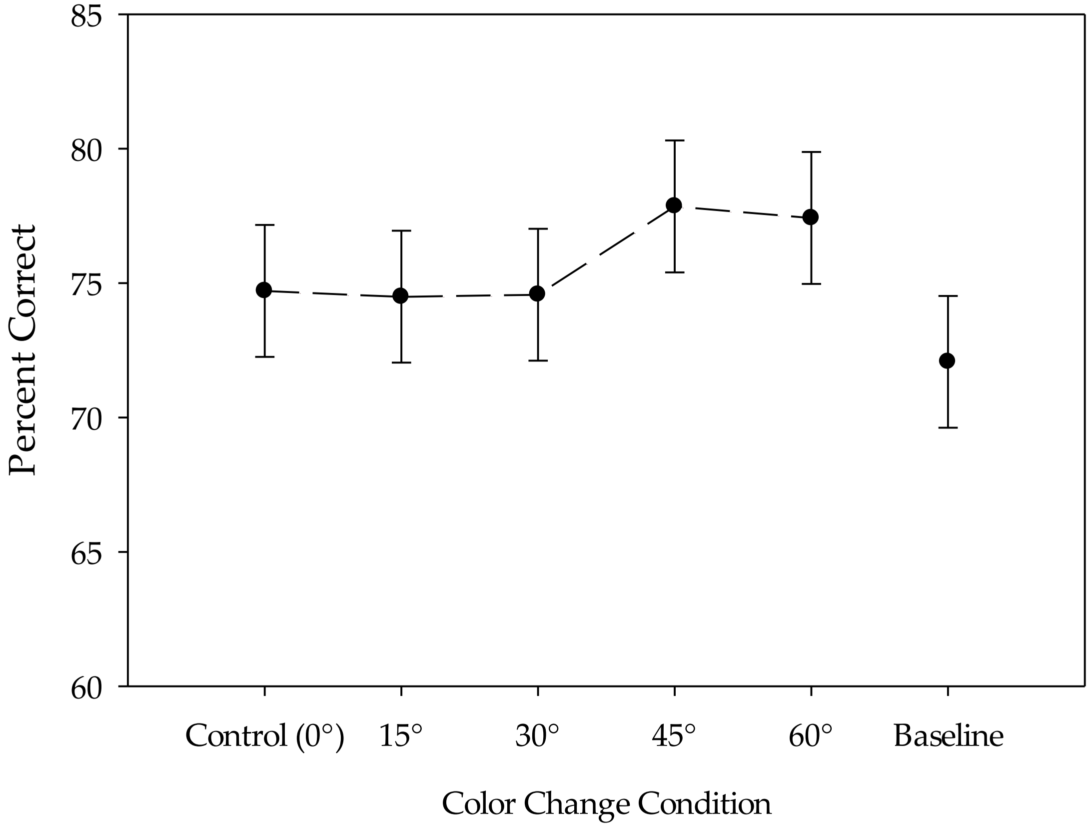

Figure 3.2. Mean accuracy in the displacement detection task as a function of conditions of Experiment 1A. In each data figure, error bars represent 95% confidence interval calculated using the within-subject design method (Franz & Loftus, 2012; Loftus & Masson, 1994).

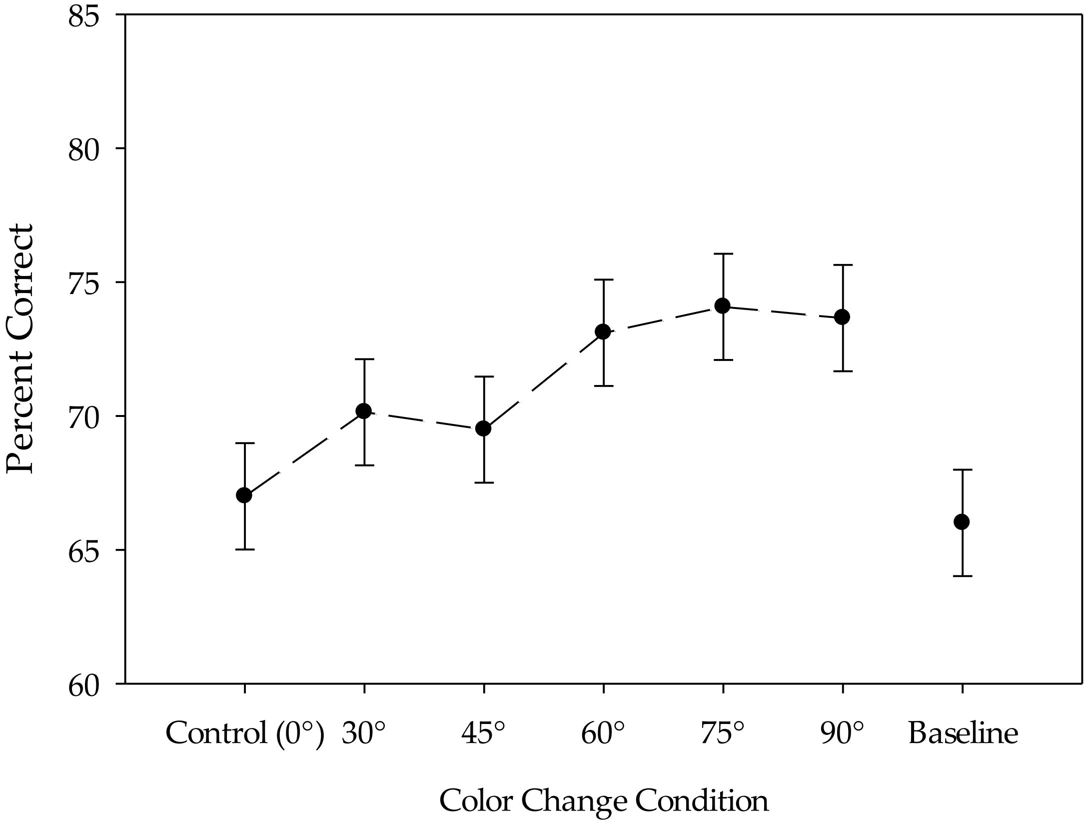

Figure 3.3. Mean accuracy in the displacement detection task of Experiment 1B.

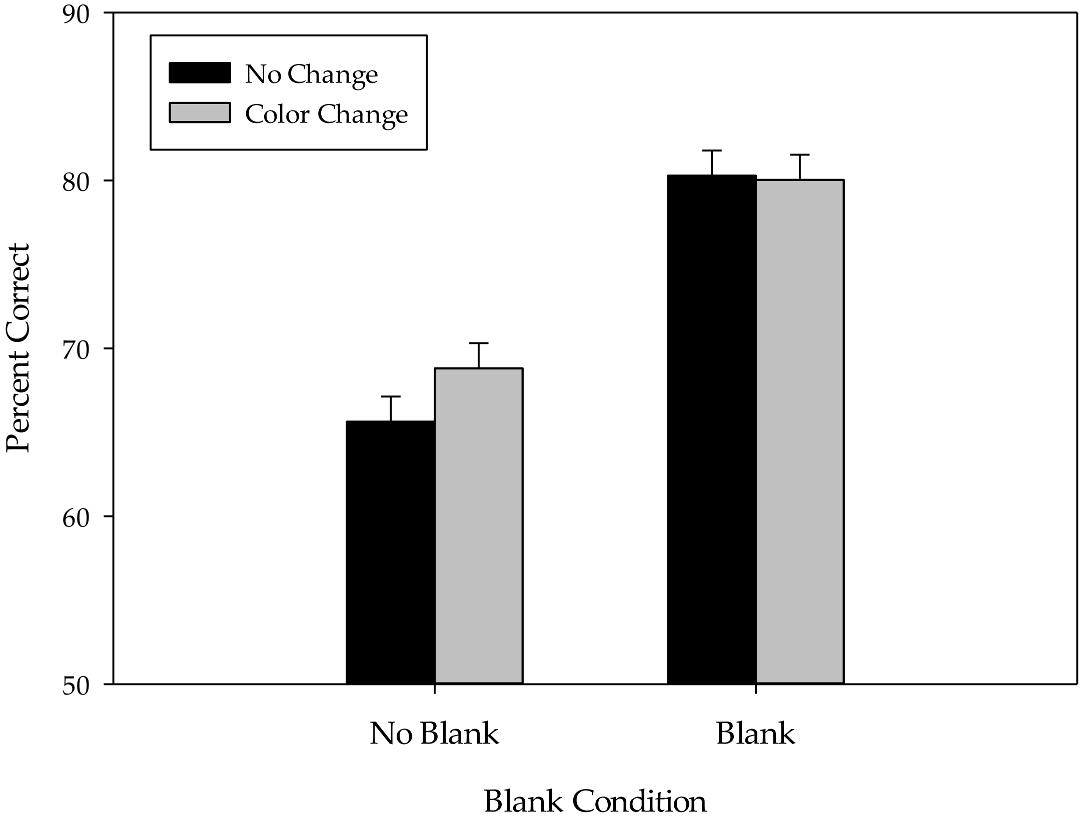

Figure 3.4. Mean accuracy in the displacement detection task of Experiment 2A.

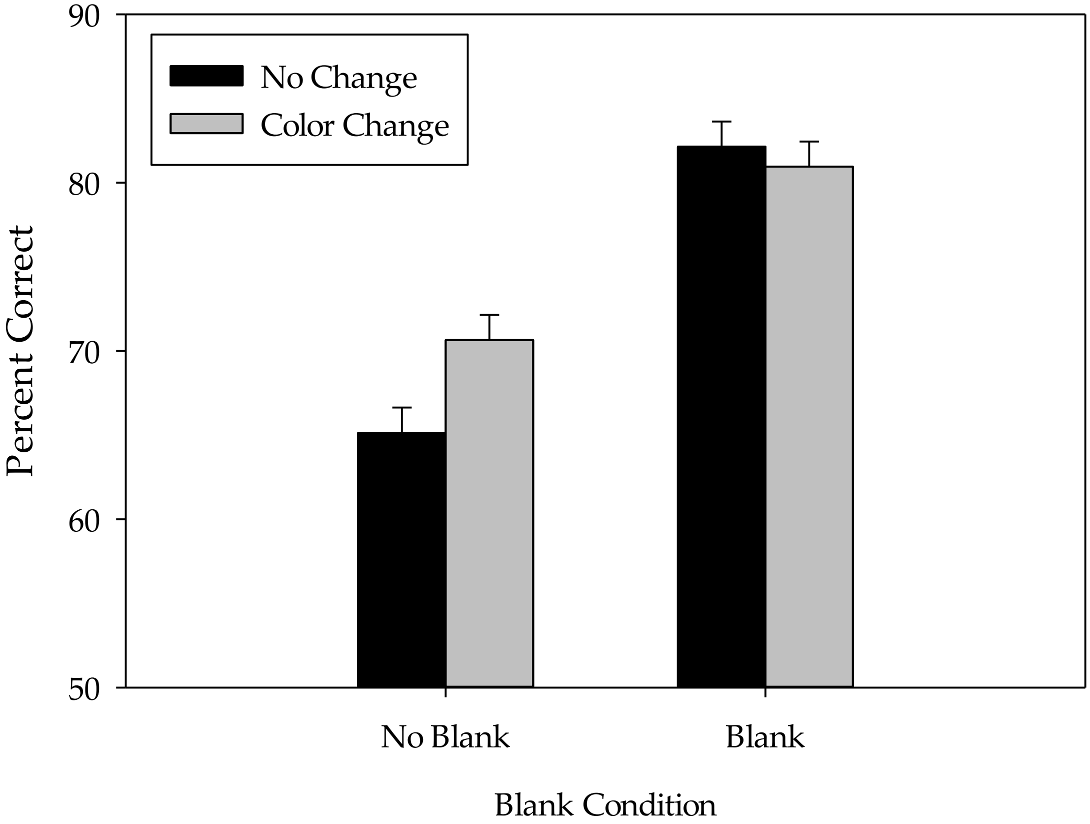

Figure 3.5. Mean accuracy in the displacement detection task of Experiment 2B.

CHAPTER IV

THE EFFECT OF VISUAL STABILITY ON THE REPRESENTATION OF THE SACCADE TARGET OBJECT

Experiments 3-6

The aim of the following experiments was to investigate the mechanism of transsaccadic object updating. Chapter 2 reviewed three broad hypotheses regarding the relationship between transsaccadic object continuity and the manner in pre- and post-saccadic representations of the saccade target object are related to each other. The experiments in this main section of the dissertation employed the continuous report method detailed in Chapter 2. Specifically, participants reported the color of either the pre- or post-saccadic versions of the saccade target object. To test different predictions regarding the role of object correspondence in object updating, the continuity of the target was manipulated with two different methods: blanking and color change. The blanking method was used as the main manipulation of object continuity. I predicted that blanking the target would disrupt stability on almost every trial, because it introduces a strong object discontinuity. In addition, for large color change magnitudes, there will be trials in which object continuity will fail. Therefore, in Experiments 5 and 6, where the magnitudes of color change were 60° and 75°, respectively, color change will act as a more subtle manipulation to disrupt visual stability. For this reason, the results of Experiments 5 and 6 were presented separately when necessary.

The first set of predictions concerns whether the pre-saccadic information is completely overwritten by the post-saccadic information, as suggested by the object-mediated updating framework. Recall that, on trials in which visual stability was disrupted by blanking the target object, I predicted that participants should have no difficulty reporting the color value of both pre- and post-saccadic disks. As a result, there should be two distributions for these blanking trials, one centered on the pre-saccadic value and another one centered on the post-saccadic value. For trials in which visual stability is established and the target is perceived as continuous, object-mediated updating predicts that the features of the pre-saccadic object would be overwritten by the post-saccadic object. In this case, participants should have limited access to the pre-saccadic color value and are therefore expected to incorrectly report the post-saccadic color value when asked to report the pre-saccadic color value on a substantial proportion of trials.

The second set of predictions concerns the integration model. If object continuity is established, then under this view, the pre- and post-saccadic representations are integrated, yielding a single representation of the color that will lie somewhere between the pre- and post-saccadic colors. The precise color value of this integrated representation will depend on the relative weighting of the two colors in the integration process. If such integration is an automatic consequence of maintaining a persisting object representation, then on no-blank trials with relatively small color change, participants should consistently report color values that lie between the pre- and post-saccadic colors, and the distribution of color responses should be similar when reporting the pre-saccadic color and the post-saccadic color.

The third set of predictions concerns the multiple states model, in which separate perceptual states of the object are maintained, despite the fact that object continuity has been established. In this case, I should observe two separate distributions of responses, one for the pre-saccadic reports and the other for the post-saccadic reports. These discrete representations may also interact with each other. For instance, it is possible that the post-saccadic state will be stronger than the pre-saccadic state because it is perceived foveally, resulting in pre-saccadic reports shifting toward the post-saccadic value. Other possibilities were discussed in Chapter 2 (see Figure 2.4).

Method

Participants. Twenty-seven participants completed Experiment 3, twenty participants completed Experiment 4, and twenty-one participants completed Experiments 5 and 6 in exchange of course credit. All reported normal or corrected-to-normal vision, and none of them reported color blindness. Participants in Experiments 4, 5, and 6 were also tested for color blindness with the 14-plate version of Ishihara color blindness test. Eight participants in Experiment 3, two in Experiment 4, three in Experiment 5, and two in Experiment 6 were eliminated from the analyses due to problems with eye calibration. The final analyses contained 19 participants in Experiments 3 and 6, and 18 participants in Experiments 4 and 5.[4]

Stimuli. The characteristics of the display and stimuli were the same as in the previous experiments, except for the differences noted. Color values were chosen with the same method as described before. In no-change trials, the color of the disk remained the same throughout the trial. In the color-change trials, the color of the post-saccadic disk was changed 30° in Experiment 3, 45° in Experiment 4, 60° in Experiment 5, and 75° in Experiment 6, either CW or CCW in the color space. The color wheel that was used to collect responses was an annulus with an outer radius of 7° and an inner radius of 3°. I created 360 color wheels which were rotated in steps of 1°. To eliminate spatial response biases, the orientation of the color wheel was chosen randomly on each trial.

Procedure. The design was a 2 (Color Change: No-change, Change) x 2 (Visual Stability: No-Blank, Blank) x 2 (Reported Object: Pre-saccadic, Post-saccadic) within-subjects design in all of the experiments. The sequence of events in a sample trial is depicted in Figure 2.1. The procedure was the same in Experiments 3-6 unless noted otherwise.

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[4] Sample size analyses revealed that a minimum of 18 participants is needed to achieve a power level of .90 with an effect size (η^2) of .40 for a 2x2x2 design experiment.

Each trial started with a black fixation cross at the center of the screen, and participants were instructed to fixate the cross. After a random delay of 1000-1500 ms, the pre-saccadic object appeared either at the left or right of the fixation. The eccentricity of the pre-saccadic disk was randomly chosen from values between 5°-7°. Participants were instructed to perceive and remember the color of this pre-saccadic disk and execute a saccade to the disk as quickly as possible. For *no-change* trials, the disk's color remained the same throughout the trial. For *color-change* trials, the post-saccadic disk's color value differed 30°, 45°, 60°, or 75° from the pre-saccadic color in Experiments 3, 4, 5, and 6, respectively. In the *no-blank* condition (NB), the color change occurred when the eye tracker detected that the eye crossed a 1.5° of visual angle boundary from the center of the screen. Therefore, the eyes landed on a differently colored disk, after the completion of the saccade. For trials in the *blank* condition (B), the screen was blanked for 250 ms after the eye tracker detected the boundary crossing, leading to the eyes landing on an empty screen after the completion of the saccade. After the blank period, the post-saccadic disk appeared at the same location as the pre-saccadic disk, either in the same color as the pre-saccadic disk (no-change trials) or in a new color (color-change trials).

In Experiment 3, the post-saccadic disk stayed on the screen for 500 ms, whereas in the other experiments the timing depended on the saccadic reaction time of the previous trial. This change was done to equate the exposure durations of the pre- and post-saccadic disks so that the findings could not be attributed to differences in mere exposure to each color. In each trial, participant's saccade latency was recorded and the saccade latency of trial n was used as the duration of the post-saccadic disk on trial n+1. The duration of the post-saccadic disk for the first trial of Experiments 4-6 was 260 ms, which was the average saccade latency in Experiment 3. In addition, if the latency was less than 150 ms or more than 700 ms in a particular trial, 260 ms was used in the subsequent trial. Although this method does not equate durations of pre- and post-saccadic disks on the same trial, it allows the durations to be similar across the full experiment.

In Experiments 4-6, participants' gaze was monitored at the beginning of each trial to ensure that they were fixating the center of the screen. If participants moved their eyes before the saccade target appeared, then a red screen was presented indicating an incorrect trial, and that trial was aborted and repeated. On average, 9%, 9%, and 6% of the trials were repeated in Experiments 4, 5, and 6, respectively.

At the end of each trial, the color wheel was presented with instructions about which object's color they need to report. Half the trials had instructions to report the color of the pre-saccadic disk ("Report the first color"), and the remaining half instructed participants to report the color of the post-saccadic disk ("Report the second color”). Participants responded by using a mouse to click the remembered value on the color wheel. The color wheel stayed on the screen until participants made a response.

In all experiments, participants first completed 8 practice trials which were not included in the analyses. For the experimental block, they completed 60 trials in each of the 8 conditions, leading to 480 trials. The experiment lasted for about 1.5 hrs.

Data Analyses and Data Fitting. In the following analyses, participants’ color response distributions were fitted with probabilistic mixture models (Bays, Catalao, & Husain, 2009). Different hypotheses were tested with different models. The full model used for the color-change trials can be formulized as follows:

$$p(x) = p_t \phi_{\mu_t,\kappa_t}(x - \theta_t) + p_d \phi_{\mu_d,\kappa_d}(x - \theta_d) + {}^{p_r}/_{2\pi}$$

where x, θ_t, and θ_d refer to the reported color value, color value of the target disk, and color value of the distractor disk, respectively. These data were entered as radians into the analyses, but were converted to degrees for presentation and visualization in the figures. In these color-change trials, the target and distractor were determined by the task. That is, if a participant was asked to report the pre-saccadic color then the pre-saccadic disk’s color value was assigned as the target color while the post-saccadic disk’s color value was assigned as the distractor color. The reverse was true for trials in which participants were asked to report the post-saccadic color. The reported color value was calculated in terms of a difference score from the target value. The target color was always represented at 0°. The distractor color value was aligned at the positive side[5], and was represented at 30°, 45°, 60°, and 75°, in Experiments 3, 4, 5, and 6, respectively.

In the model, $\phi_{\mu,\kappa}$ refers to the probability density function (pdf) of von Mises distribution with a mean of μ and a concentration of κ ($SD = \sqrt{1/\kappa}$). von Mises distribution is the circular analog of the Gaussian distribution (Bays et al., 2009; Best & Fisher, 1979), and is more appropriate to use for the current analyses because the color values were drawn form a circular space during the experiments. Lastly, p_t, p_d, and p_r refer to probability of reporting the target color, distractor color, and a random color value, respectively. Note that $p_t + p_d + p_r = 1$. Maximum likelihood estimates of the parameters for each model were calculated using MatLab's *mle* function, which uses the non-linear optimization procedure (*fminsearch* function) created by Nelder and Mead (1965).

The no-change trials were run as the control condition; that is, to measure a baseline performance level for the current task. Data from these no-change trials were fit with the following model:

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[5] All analyses were first run separately for the two change direction conditions (CW and CCW). The pattern of results did not differ between the two conditions; therefore, the data were collapsed for all the analyses reported here.

$$p(x) = p_t \phi_{\mu_t,\kappa_t}(x - \theta_t) + {}^{p_r}/_{2\pi}$$

where there is one von Mises distribution representing the target distribution and a uniform distribution representing the reports of a random color value. In the equation, $p_t + p_r = 1$.

Recently, Golomb et al. (2014) reported a study that used similar probabilistic mixture model analyses to test similar hypotheses in a different domain. As mentioned in Chapter 2, their experiments did not directly test the representation of the saccade target object. Instead, they investigated how distractors presented at different locations affect the representation of a pre-cued target. For their analyses, they used the same versions of the model used in the analyses described below. For instance, they used the fixed models discussed in the overwriting results below to test the probability of incorrectly reporting the distractor value (swapping). Similarly, they used the flexible models described in the feature interaction section to test distribution shifts. An important difference between their analyses and the current dissertation is the method used to examine systematic biases in a remembered color value. In their experiments, Golomb et al. (2014) did not have a separate control condition: Participants always reported the cued color. To analyze their data, they took a particular distribution of color value responses around the actual value and compared the report probability of values on one side of the distribution with the report probability of corresponding values on the other side, with the logic that if the distribution had shifted or was otherwise altered, there would be a systematic pairwise difference between the probability of report at corresponding values on either side of the true value (see Figure 4.1 for details). There are several limitations to this method that led us to employ a different analytical approach. First, the multiple pairwise tests were not corrected for multiple comparisons, which significantly increases the likelihood of incorrectly rejecting a true null hypothesis, that is, probability of making a Type I error (Shaffer, 1995). In addition, given that the probability data at each color value were drawn from a single probability distribution, observations entering into the comparisons were not independent. Even without proper correction and with non-independent samples, most of their analyses resulted in marginally significant results. For instance, to test their *swapping* (overwriting) prediction, they ran a paired-sample t-test to compare the data centered on the distractor color (+90°) with the data on its corresponding opposite location (-90°). The results showed a marginally significant effect in Experiment 1 (p = .046) and a significant effect in Experiment 3 (p =.009). Since the authors ran 14 different pairwise comparisons for each experiment, the appropriate α level with Bonferroni correction for rejecting the null hypothesis is .003 which would result in a non-significant result even in Experiment 3.

In contrast to the approach of Golomb et al. (2014), in the analyses below I always compared trials from different conditions. For instance, to test the overwriting hypothesis, I compared the no-blank and blank trials for pre-saccadic and post-saccadic reports separately. In addition, all of the pairwise comparisons mentioned below used Bonferroni correction to minimize false rejections of the null hypothesis (Dunn, 1961).

Results

Elimination of error and outlier trials. For Experiment 3, I first calculated the total fixation duration in the center area, defined as 1.5° of visual angle area around the fixation cross, before the onset of the target disk. Trials on which participants made multiple fixations within this center region were included in the analyses. However, a trial was eliminated if the eyes moved away from the fixation area before the presentation of the target disk. This resulted in elimination of 3% of trials. Since Experiments 4-6 included a saccade-contingent feedback at the beginning of each trial as described above, no trial was eliminated for this reason. Trials in which the saccade latency to the disk was less than 100 ms (3%, 2%, 2%, 1% of the trials in Experiments 3, 4, 5, and 6, respectively) or longer than 2.5 standard deviations above the mean (735 ms; 3% of the trials in Experiment 3, 475 ms; 3% of the trials in Experiment 4, 595 ms; 1% of the trials in Experiment 5, and 665 ms; 1% of the trials in Experiment 6) were also eliminated. In the end, a total of 9%, 5%, 3%, and 2% trials were excluded from the analyses in Experiments 3, 4, 5, and 6, respectively.

Testing the integration hypothesis. Figures 4.2 and 4.3 show the frequency of color responses as a function of color values, separately for no-blank and blank conditions. The dashed lines represent the target value at 0° and the distractor value at the positive side (+30°, +45°, +60°, and +75°). I first evaluated whether the pre- and post-saccadic representations were merged into a single distribution, with a distribution mean somewhere between the two color values, as predicted by the integration model. Recall that, if the visual system integrates two colors of the same object, then the precise feature values of the objects should be lost, and participants should report a value that is somewhere between the pre- and post-saccadic color, regardless of whether they are asked to report the pre- or the post-saccadic color. As can be seen in Figures 4.2 and 4.3, this was not the case. When asked to report the post-saccadic color value (purple lines), participants' color reports were centered precisely on the correct value for both no-blank (Figure 4.2) and blank (Figure 4.3) trials. For trials in which participants reported the pre-saccadic color (green lines), the distributions were more complex, particularly for the no-blank trials. Yet, for a substantial majority of the trials, participants accurately reported the pre-saccadic color, resulting in a distribution centered on the pre-saccadic color value. These findings demonstrate that participants can successfully retain the pre- and post-saccadic feature values independently, disconfirming the integration hypothesis. However, for the pre-saccadic reports, the data showed a second distribution centered on the post-saccadic color, consistent with overwriting of the pre-saccadic color by the post-saccadic color.

Testing the overwriting hypothesis. To test the overwriting hypothesis, I first calculated the probabilities of reporting the distractor color in each condition, and determined the proportion of trials in which participants reported the post-saccadic color instead of the pre-saccadic color. As converging evidence, data from the color-change trials were fit to both a unimodal and a bimodal distribution. The fits from these two models were compared to test whether conditions in which overwriting was observed were better explained by a bimodal than a unimodal model.

Analyses of p_t, p_d, *and* p_r. For each experiment and each condition, I first used the full model described above to obtain the probabilities of reporting the target, distractor, and a random color value. In each model, there were three separate distributions: two Gaussians representing the target and the distractor distributions and a uniform distribution representing the reports of a random color value. In each model, the means of the target and the distractor distributions were fixed. For instance, for Experiment 3, the target mean was at 0°, and the distractor mean was at 30°. Each model had four free parameters: probability of reporting the distractor color (p_d), probability of reporting a random color (p_r), and concentrations (i.e., standard deviations) of the target and distractor distributions. Probability of reporting the target color was calculated as

$$p_t = 1 - (p_d + p_r)$$

Models were fit separately for each participant. Figure 4.4 shows best-fit values for p_t, p_d, and p_r parameters averaged across participants. First, when visual stability was not disrupted (no-blank), on 31% of the trials in Experiment 3 and on 25% of the trials in Experiment 4, participants incorrectly reported the post-saccadic color when asked to report the pre-saccadic color. When visual stability was disrupted with a blank; however, participants should have produced a substantially smaller proportion of incorrect post-saccadic color responses in both experiments. These differences were supported by the analyses. For both experiments, separate ANOVAs were run on $p_d$data with Blank (no-blank, blank) and Report (pre-saccadic, post-saccadic) as within-subject factors. The results showed a significant main effect of Blank, $F(1,18) = 25.36$, $p < .001$ in Experiment 3 and $F(1,17) = 23.66$, $p < .001$ in Experiment 4, a significant main effect of Report, $F(1,18) = 19.35$, $p < .001$ in Experiment 3 and $F(1,17) = 28.13$, $p < .001$ in Experiment 4, and a significant Blank x Report interaction, $F(1,18) = 44.79$, $p < .001$ in Experiment 3 and $F(3,51) = 11.56$, $p = .003$ in Experiment 4. Bonferroni corrected pairwise comparisons showed significantly larger p_d values for no-blank trials (NB_Pre) than for blank trials (B_Pre) when participants were asked to report the pre-saccadic color, $t(18) = 6.45$, $p < .001$ in Experiment 3 and $t(17) = 4.59$, $p < .001$ in Experiment 4. These differences were not significant for trials where participants were asked to report the post-saccadic color (NB_Post vs B_Post; *t*s < 1; *p*s > .20). p_d values in these post-saccadic report trials ranged between 5%-8% across the experiments. This indicates a baseline error rate of approximately 7%, in which participants either misunderstood the instructions for the report or confused the pre- and post-saccadic colors.

As discussed in Chapter 3, visual stability is more substantially disrupted if the magnitude of color change between the pre- and post-saccadic objects is larger than 60°. Therefore, it is likely that the color change by itself induced instability in significantly more trials in Experiments 5 and 6 than in Experiments 3 and 4. Consistent with this prediction, overwriting only occurred on 15% of the trials in Experiment 5 and 13% of the trials in Experiment 6. Repeated-measures ANOVA showed significant main effects of Blank in both Experiment 5, $F(1,17) = 5.30$, $p = .034$, and Experiment 6, $F(1,18) = 5.02$, $p = .038$. The main effect of Report was marginally significant in Experiment 5, $F(1,17) = 4.66$, $p = .045$, but not in Experiment 6, $F(1,18) = 1.51$, $p = .24$. Similarly, a significant Blank x Report interaction was found in Experiment 5 but not in Experiment 6, $F(1,17) = 6.03$, $p = .025$, and $F < 1$, respectively. Bonferroni corrected comparisons revealed a significantly larger p_d values for no-blank than for blank trials for pre-saccadic color reports in both Experiments 5 and 6, $t(17) = 2.67$, $p = .02$ and $t(18) = 2.72$, $p = .014$, respectively.

These results are compatible with the results of Chapter 3: As the color distance increases, the probability of the color change disrupting stability increases, leading to a lower probability of overwriting. In fact, the blanking effect decreased as the magnitude of color change increased. The differences in p_d values between the no-blank and blank conditions were 18%, 13%, 7%, and 4% in Experiments 3-6, respectively, providing converging evidence for the relationship between the magnitude of color change and visual stability.

An alternative explanation for the higher proportions of overwriting in Experiments 3 and 4 is that when the colors are similar, participants had uncertainty about which state to report. Specifically, the probability of overwriting in all experiment might be the same, but as the distance between the pre- and post-saccadic color decreases, participants may have a higher probability of confusing the two colors, generating a greater proportion of pre-saccade report trials on which they reported the post-saccadic color. If this is true, then a similar increase in incorrect reports should be observed for trials in which participants reported the post-saccadic color in Experiments 3 and 4. To test this alternative explanation, I compared the $p_d$values for trials in which participants reported the post-saccadic color across the experiments. I ran two one-way

ANOVAs to compare the p_d values for post-saccadic reports of no-blank and blank conditions separately. The results revealed no significant difference between the experiments for both no-blank and blank conditions, $F(3,70) = 1.15$, $p = .34$ and $F < 1$, respectively. Thus, the data are more consistent with the idea that the color difference in Experiments 5 and 6 led to disruption of stability, which decreased the incidence of overwriting.

I also tested whether the precisions of the distributions depend on visual stability. The standard deviations for the target and the distractor distributions were free parameters in the model described above (see Figure 4.6). Separate 2 (Blank: no-blank, blank) x 2 (Report: pre-saccadic, post-saccadic) repeated-measures ANOVAs were run on the best-fit standard deviation values of the target and distractor distributions for each experiment. For the target distributions, the results showed a significant main effect of Report in all experiments, $F(1,18) = 15.05$, $p = .001$ in Experiment 3; $F(1,17) = 35.89$, $p < .001$ in Experiment 4; $F(1,17) = 38.03$, $p < .001$ in Experiment 5; and $F(1,18) = 16.62$, $p = .001$ in Experiment 6. Specifically, color reports for the post-saccadic object had higher precision (i.e. smaller standard deviations) than for the pre-saccadic object. Neither the main effects of Blank nor the Blank x Report interactions were significant (all ps > .05). None of the distractor distribution effects was significant (all ps > .05). These findings suggest that the memory for a peripheral pre-saccadic color is less precise than the memory of a foveal post-saccadic color. This is consistent with the findings that color sensitivity decreases as the eccentricity increases (O'Regan, 1992) and with the fact that the post-saccadic color was the more recently presented of the two.

Overall, these results suggest that when visual stability was likely to have been established (no-blank trials with relatively small color change), the color of the pre-saccadic object was overwritten by the color of the post-saccadic object, but only on a moderate to small proportion of trials, supporting a partial overwriting hypothesis. The probability of overwriting was also affected by the magnitude of color change. The p_d values decreased as the distance between the pre- and post-saccadic colors increased. This decrease is most likely due to disruptions of visual stability created by color change alone. A second finding was that standard deviations did not differ between no-blank and blank conditions, indicating that the manipulation of visual stability only affected the probability of overwriting but not the precision of the memory for the pre-saccadic object.

Comparison with the control (no-change) condition. As discussed above, the data from the no-change trials were fit with a unimodal Gaussian distribution plus a uniform distribution. The best-fit parameter values for p_t and p_r were given in Figure 4.5. As reflected in the figure, the reports were very accurate in these control conditions.

Standard deviation fits of the no-change and color-change trials were plotted in Figure 4.6. For each experiment, I ran four Bonferroni corrected *t*-tests on the standard deviation fits to investigate whether adding a distractor color affected the precision of the target color distribution. I hypothesized that the presence of a second color would decrease the precision of the target distribution, leading to larger standard deviation values for color-change trials than for no-change trials. For trials where visual stability was disrupted with a blank, the target color may be less likely to be affected by the presence of a distractor color; therefore, may be represented with high precision. For blank trials, I predicted to find no significant difference between the standard deviations of color-change and no-change trials.

The following analyses focused only on trials where participants were asked to report the pre-saccadic color. Similar results were found for post-saccadic color reports. For trials where visual stability was not disrupted (no-blank), there was no significant difference between no-change and color-change conditions in Experiment 3, $t(18) = 1.71$, $p = .11$. For the remaining experiments; however, this difference was significant, $t(17) = 2.62$, $p = .018$ in Experiment 4, $t(17) = 4.64$, $p < .001$ in Experiment 5, and $t(18) = 7.11$, $p < .001$ in Experiment 6. When visual stability was disrupted with a blank, no-change and color-change conditions showed similar standard deviations in Experiments 3 and 4 (*t*s < 1 and *p*s > .80). However, the no-change condition resulted in significantly smaller standard deviations than the color-change condition for larger color change separations, $t(17) = 5.22$, $p < .001$ in Experiment 5 and $t(18) = 8.70$, $p < .001$ in Experiment 6.

As predicted, changing saccade target's color decreased the precision of both pre- and post-saccadic color representations. The only exception was Experiment 3 in which the target and the distractor colors were close in color space (30°); therefore, the target and distractor response distributions were not distinct (see Figure 4.2). In this case, it is possible that the model could not accurately estimate the standard deviations of the target and distractor distributions because of the amount of the overlap created by the close proximity. When visual stability was disrupted by a blank, the precision of the target color response was not affected by the presence of a distractor color for smaller target-distractor separations. For larger separations, the additional color decreased the precision of the target-related response. Although it is not clear why different experiments led to different results for these blank trials, one possible explanation is that larger color changes could result in less precise representations for both colors, regardless of visual stability. As can be seen in Figure 4.6, in almost all conditions standard deviations for Experiments 5 and 6 were larger than standard deviations for Experiments 3 and 4. To test this possibility, I compared standard deviations of each experiment with one-way ANOVAs separately for each condition. The experiments significantly differed from each other for all conditions, $F(3,70) = 4.87$, $p = .004$ for

NB_Pre, $F(3,70) = 8.56$, $p < .001$ for NB_Post, $F(3,70) = 11.15$, $p < .001$ for B_Pre, and $F(3,70) = 6.30$, $p = .001$ for B_Post. Bonferroni corrected post-hoc tests showed significantly larger standard deviations in Experiment 6 compared to Experiments 3 and 4 for all conditions. Standard deviations in Experiments 5 and 6 did not differ in any condition. These results suggest that as the distance between the pre- and post-saccadic colors increased the distributions became wider, resulting in larger standard deviations.

Unimodal versus bimodal distributions. The fixed-mean models described above showed significantly more trials in which overwriting occurred in no-blank than in blank trials. As converging evidence, I also tested whether each color-change distribution was fit better by a unimodal or a bimodal distribution. Specifically, if participants were more likely to report the post-saccadic color instead of the pre-saccadic color under stability (i.e., overwriting) then the no-blank/color-change condition should fit better by a bimodal distribution than a unimodal distribution. For the remaining conditions, I expected to find better fits by a unimodal distribution. To quantify model fits, Akaike Information Criterion (AIC) was calculated for each model (Akaike, 1974). The standard AIC formula is:

$$\mathrm{AIC} = 2k - 2\ln(L)$$

where k is the number of parameters included in the function and L denotes the maximum likelihood value of the function. The model with the smallest AIC value is considered as the best description of the data. In the following analyses, I calculated AICc, which corrects the criterion for a small sample size (Burnham & Anderson, 2004). The formula for AICc is as follows:

$$\mathrm{AICc} = AIC + 2k\,(k-1)/(n-k-1)$$

where n is the sample size. AIC is more appropriate to determine the best model than maximum likelihood because it eliminates the problem of overfitting. That is, as the model becomes more complex by increasing the number of free parameters, the maximum likelihood will increase, showing better fits. AIC, instead, penalizes for adding a free parameter. Therefore, it is a better measure to compare models with different numbers of free parameters than the maximum likelihood.

For each experiment, I ran two separate models: a unimodal model, with the mean of the target distribution fixed at 0° and the standard deviation of the target distribution as a free parameter; and a bimodal model, with fixed target (0°) and distractor distributions means (30°, 45°, 60°, or 75°) and the standard deviations of the target and distractor distributions as free parameters. The formulae for the unimodal and bimodal models are as follows:

$$p(x) = \phi_{\mu,\kappa}(x - \theta)$$

$$p(x) = p_t \phi_{\mu_t,\kappa_t}(x - \theta_t) + \ p_d \phi_{\mu_d,\kappa_d}(x - \theta_d)$$

Note that the uniform distribution representing the probability of reporting a random color was eliminated from these analyses. In addition, I ran these models with a uniform distribution but the fits were not significantly improved compared to the no-uniform versions used for the current analyses. Specifically, I ran separate t-tests to compare the AIC values of the uniform and no-uniform models, for all four conditions separately (NB_Pre, NB_Post, B_Pre, B_Post) for Experiments 3-6. Out of 16 paired-samples t-tests, 5 showed a significant advantage for the no-uniform distribution while the remaining 11 showed no significant difference. Since I did not find convincing evidence for adding an extra parameter to the models, I chose to use the more parsimonious version of the models. To ensure that eliminating the uniform distribution did not alternate the findings, I additionally ran all the following analyses with the uniform models. The pattern of results did not differ between those two.

To test whether the data fit better to a unimodal than a bimodal model, I ran separate 2 (Model: unimodal, bimodal) x 2 (Blank: no-blank, blank) x 2 (Report: pre-saccadic, post-saccadic) ANOVAs for each experiment on the AIC values. Results showed a significant main effect of Report, significant Model x Blank, Model x Report, and Model x Blank x Report interactions for Experiment 3, $F(1, 18) = 42.70$, $p < .001$, *F*(1,18) = 32.55, *p* < .001, *F*(1, 18) = 7.33, *p* = .014, and *F*(1,18) = 38.01, *p* < .001 respectively. Other main effects and interactions were not significant. For Experiment 4, the main effect of Report, Model x Blank and Model x Blank x Report interactions were significant, *F*(1,17) = 86.66, *p* < .001, *F*(1, 17) = 45.95, *p* < .001, and *F*(1,17) = 38.46, *p* < .001, respectively. For Experiment 5, the main effects of Model and Report and the three-way interaction were significant, *F*(1,17) = 8.46, *p* = .01, *F*(1, 17) = 19.24, *p* < .001, and *F*(1,17) = 6.23, *p* = .023, respectively. Finally, for Experiment 6, the main effects of Model, Blank, and Report, and Model x Blank and Model x Blank x Report interactions were significant, *F*(1,18) = 8.82, *p* =. 008, *F*(1, 18) = 4.71, *p* = .044, *F*(1,18) = 9.04, *p* = .008, *F*(1,18) = 9.02, *p* = .008, and *F*(1,18) = 10.64, *p* = .004, respectively. To explain the three-way interactions, four Bonferroni corrected pairwise *t*-tests were run for each experiment (*p* = .0125). The comparisons showed that in all experiments the bimodal model had significantly better fits than the unimodal model for the NB_Pre trials, *t*(18) = 5.60, *p* < .001, *t*(17) = 3.90, *p* = .001, *t*(17) = 5.40, *p* < .001, *t*(18) = 4.89, *p* < .001, in Experiments 3-6 respectively. Conversely, B_Pre trials showed better fits (i.e. smaller AIC values) to the unimodal than to the bimodal model in all experiments. This effect was significant in Experiments 3 and 4, *t*(18) = 4.17, *p* = .001, *t*(17) = 2.99, *p* = .008, respectively. For the post-saccadic reports, the distributions were better fit to a bimodal than to a unimodal model in all experiments. This difference was only significant in Experiments 5 and 6, NB_Post: $t(17) = 5.68$, $p < .001$, $t(18) = 4.01$, $p = .001$, B_Post: $t(17) = 4.93$, $p < .001$, $t(18) = 3.97$, $p = .001$.

To summarize, these results are in line with the probability of report results: Visual stability significantly affected the representation of the pre-saccadic object. The color responses were bimodal when visual stability was established in the no-blank trials while the responses became unimodal when stability was disrupted with a blank. That is, the incorrect post-saccadic reports in the no-blank trials created a separate distribution, resulting in those conditions to be fit better with a bimodal model.

In the following feature interaction analyses, I used a bimodal model for the NB_Pre condition and a unimodal model for the B_Pre condition. For the post-saccadic conditions (NB_Post, B_Post), it is surprising that the distributions were better fit by a bimodal model even though this effect was not significant in Experiments 3 and 4. To ensure that the results were not affected by the choice of model, I ran the shifted models both with a unimodal model and a bimodal model for B_Pre, NB_Post, and B_Post conditions. Although the exact magnitude of the effects did change depending on the model used, the statistical results and their interpretations did not differ. In the next section, I reported the results from the bimodal models for the NB_Pre, NB_Post, and B_Post conditions and from the unimodal model for the B_Pre condition.

Testing feature interaction between representations of multiple states of the same object. As discussed in the previous two sections, there was no evidence that color information was integrated across the saccade, leading to a representation of color intermediate between the pre- and post-saccadic colors. In addition, although visual stability led to some degree of overwriting, a substantial majority of trials reflected relatively accurate report of the probed color value, both for the pre-saccadic color and for the post-saccadic color. This pattern provides strong support for a model in which multiple states of the same object are represented simultaneously across a saccade. In this section, I examined whether these discrete representations interact, testing the feature interaction hypotheses discussed in Chapter 2.

First, to examine whether the target distribution was affected by the presence of the distractor color, for each condition I ran a model which estimates the mean of the target distribution. For the bimodal conditions (NB_Pre, NB_Post, B_Post), the mean of the distractor distribution was fixed (at 30 °, 45°, 60°, or 75°) and the remaining four parameters were free: p_d, μ_t, κ_t, and κ_d. For the B_Pre condition, there were two free parameters: μ_t and κ_t. To ensure that adding a free parameter (μ_t) increased the model fits, I compared the AIC values of these free-mean models with the models where the mean of the target was fixed. Results showed better fits for the free-mean models in twelve out of sixteen comparisons, validating the treatment of mean value as a free parameter.

Figure 4.7 shows the average of the best-fit μ_t parameter values. In the figure, positive values indicate a shift toward the distractor value (i.e., attraction) while negative values indicate a shift away from the distractor value (i.e., repulsion). To determine whether the means of the main distributions were shifted, I ran four Bonferroni corrected one-sample *t*-tests for each experiment separately with 0° as the test value. In Experiment 3, the means of the target distributions (μ_t) did not significantly differ from the baseline for the bimodal models (all *p*s > .10) but it did for the B_Pre condition, $t(18) = 2.86$, $p = .01$. For the remaining experiments, the means were significantly shifted toward the distractor color in all conditions (all *p*s < .01) except for the NB_Post condition in Experiment 4 ($p = .018$) and the B_Post condition in Experiment 5 ($p = .014$), where the effect was marginal. Together, these results suggest that the representation of the target object was shifted toward the distractor color value regardless of the visual stability condition and the state of the object participants reported.

In a next step, I tested if the incorrect distractor color responses (the trials where the pre-saccadic color was overwritten by the post-saccadic color) were affected by the target (i.e. pre-saccadic) color in the NB_Pre condition, in which overwriting was observed in a substantial proportion of trials. For these analyses, I ran a bimodal model on the NB_Pre data where the mean of the target distribution was fixed at 0° while the remaining four parameters were free: p_d, μ_d, κ_t, and κ_d. One-sample *t*-tests were run on the distractor means (μ_d, Figure 4.7) with 30°, 45°, 60°, and 75° as the test values in Experiments 3-6, respectively. The mean of the distractor distribution was shifted toward the target value in Experiments 4-6 but not in Experiment 3, $t(17) = -3.67$, $p = .002$, $t(17) = -3.79$, $p = .001$, $t(18) = -2.94$, $p = .009$, and $t(18) = -1.32$, $p = .20$, respectively. Together with the target mean results described above, these findings support the attraction hypothesis, where the representations of target and distractor colors were shifted toward each other.

Discussion

The results of Experiments 3-6 indicated that (1) the pre- and post-saccadic states of the target object can be represented separately, rejecting the feature integration hypothesis; (2) on a considerable proportion of no-blank trials, the pre-saccadic color value was overwritten by the post-saccadic color value, supporting the partial overwriting hypothesis; and (3) both pre- and post-saccadic reports were shifted toward each other, supporting the feature interaction hypothesis.

Specifically, when visual stability was established, on a substantial proportion of the trials, the color of the pre-saccadic object was replaced by the color of the post-saccadic object. The probability of overwriting depended on the separation between the pre- and post-saccadic colors. When the colors were relatively close (for 30° and 45° separations), participants reported the post-saccadic color in approximately 1/3 of the trials. When the distance between pre- and post-saccadic colors increased (for 60° and 75°), incorrect post-saccadic reports occurred in 15% of the trials. Comparisons of these no-blank trials with blank trials showed that the proportion of misreports significantly decreased when visual stability was disrupted with a blank, supporting the partial overwriting predictions.

Further support for the partial overwriting hypothesis came from the comparisons between unimodal and bimodal models. Under conditions of visual stability, the distribution of trials in which participants reported the pre-saccadic color showed better fits for a bimodal model than for a unimodal model. Specifically, for these trials there was one distribution centered on the pre-saccadic color value and another distribution centered on the post-saccadic color value representing the trials in which overwriting occurred. Because overwriting did not occur on every trial, it can be concluded that the strong version of the object-mediated updating framework was not supported. Nevertheless, a substantial proportion of trials showed overwriting, indicating that overwriting is in fact one of the active mechanisms by which the visual system reconciles the pre- and post-saccadic information.

Standard deviation comparisons revealed that changing the target's color generally decreases the precision of both representations. However, there was no significant difference between the no-blank and blank trials for the color-change condition, indicating that visual stability only affects the probability of overwriting but not the precision of the saccade target representation.

Results from the flexible models showed that the means of these two discrete representations were shifted toward each other. Interestingly, the distributions for the post-saccadic color reports were also shifted toward the pre-saccadic color value. A possible explanation for these mean shifts is that the actual representations of the pre- and post-saccadic states are affected by each other, as proposed in Chapter 2. That is, the visual system can successfully represent multiple states of a single object but these two discrete states dynamically interact with each other, resulting in a final representation of altered feature values for both states. Alternatively, the distributions may not be symmetrical as assumed by the Gaussian distribution. Instead, the misreports (i.e. thep_d distributions) may have skewed the distribution for the target color. Specifically, the target distribution is centered on the correct color value with a skewed tail due to the incorrect reports around the distractor value. If this is true, then averaging the reported values would result in a mean that is different than the actual value even though the mean of the distribution is not shifted. Although theoretically plausible, this result is not very likely in the current experiments. First, the mean shifts were observed in all experiments except for Experiment 3 where the highest proportion of overwriting was found (31%). If the incorrect distractor reports (i.e., overwriting trials) cause the target distribution mean to be miscalculated, I would expect to see a larger mean shift in Experiment 3 than in the other experiments. Second, significant mean shifts were also found for trials in which participants reported the post-saccadic color where thep_d values were as low as 5%. Third, the magnitudes of the mean shifts were comparable in Experiments 4, 5, and 6 (for NB_Pre: 5.6°, 4.4°, and 4.1 respectively); therefore, it is unlikely that the mean shifts were modulated by the probability of overwriting (p_d). Lastly, a significant mean shift was observed even for Experiment 6 where the target and distractor distributions were clearly separate; thus, less likely to be resulted by the misreports (see Figure 4.2). Taken together, the data suggest that the shifts in distribution means are not an artifact of the skew caused by the misreport distributions. Nevertheless, it is not possible to completely rule out this alternative explanation without testing the same models with a new distribution which takes skewness into account.

In sum, the results failed to support the hypothesis that two colors of an object are integrated across a saccade. There was support for a partial overwriting mechanism, consistent with the object mediated updating hypothesis. On the majority of trials, however, participants were able to maintain discrete representations of the pre- and post-saccadic states of the object. Further, the pre- and post-saccadic states influence each other, resulting in a systematic shift toward the other state. Implications for transsaccadic perception and updating are discussed in Chapter 5.

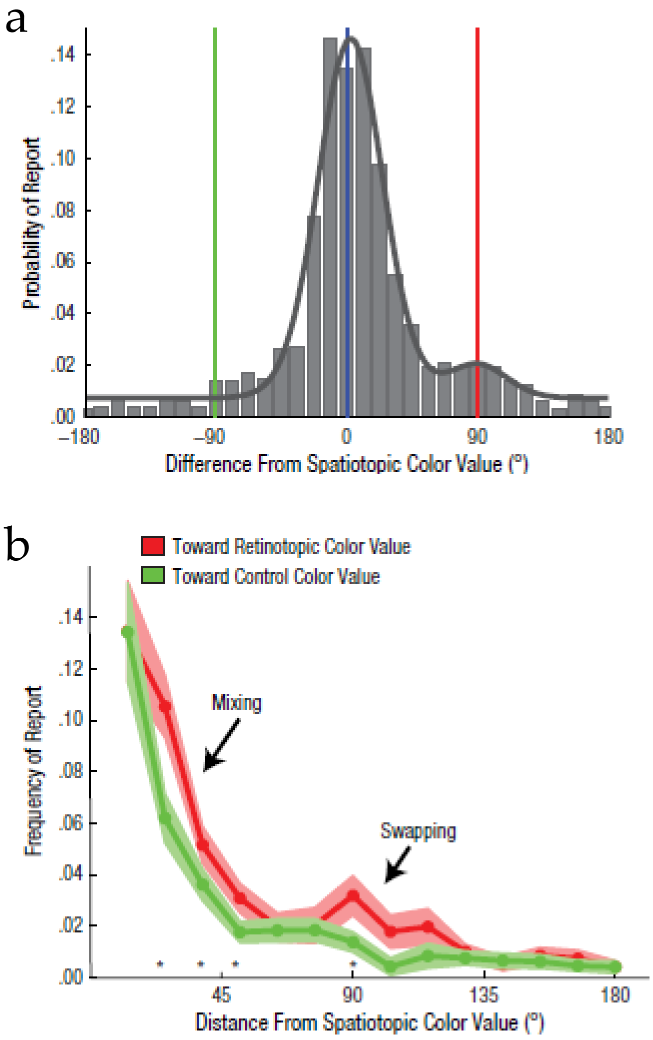

Figure 4.1. Probability of report data (a) and the analysis method (b) used in Experiment 1 of Golomb et al. (2014). Data in (a) was used to create the graph in (b). In this experiment, the target was the spatiotopic color (0° in graph (a)) and the retinotopic distractor color was at +90°. The red line in (b) is the right side of the distribution plotted in (a) while the green line is the left side of the distribution. The asterisks indicate the bins where the red line differed from the green line at $\alpha = .05$.

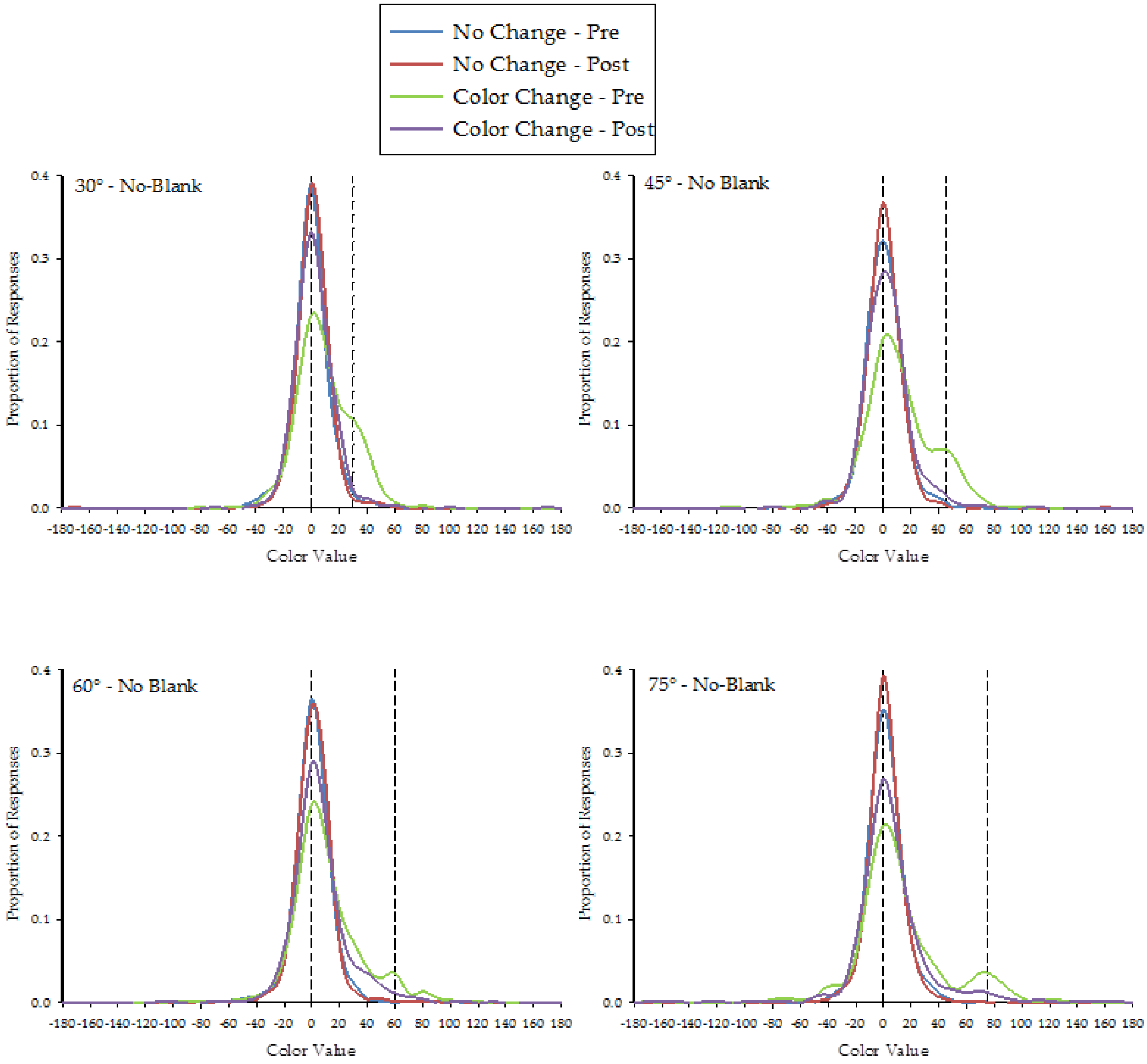

Figure 4.2. Proportion of color responses for the Stability (No-Blank) conditions of Experiments 3-6. The dashed lines represent the target color value at 0° and the corresponding distractor values in each experiment.

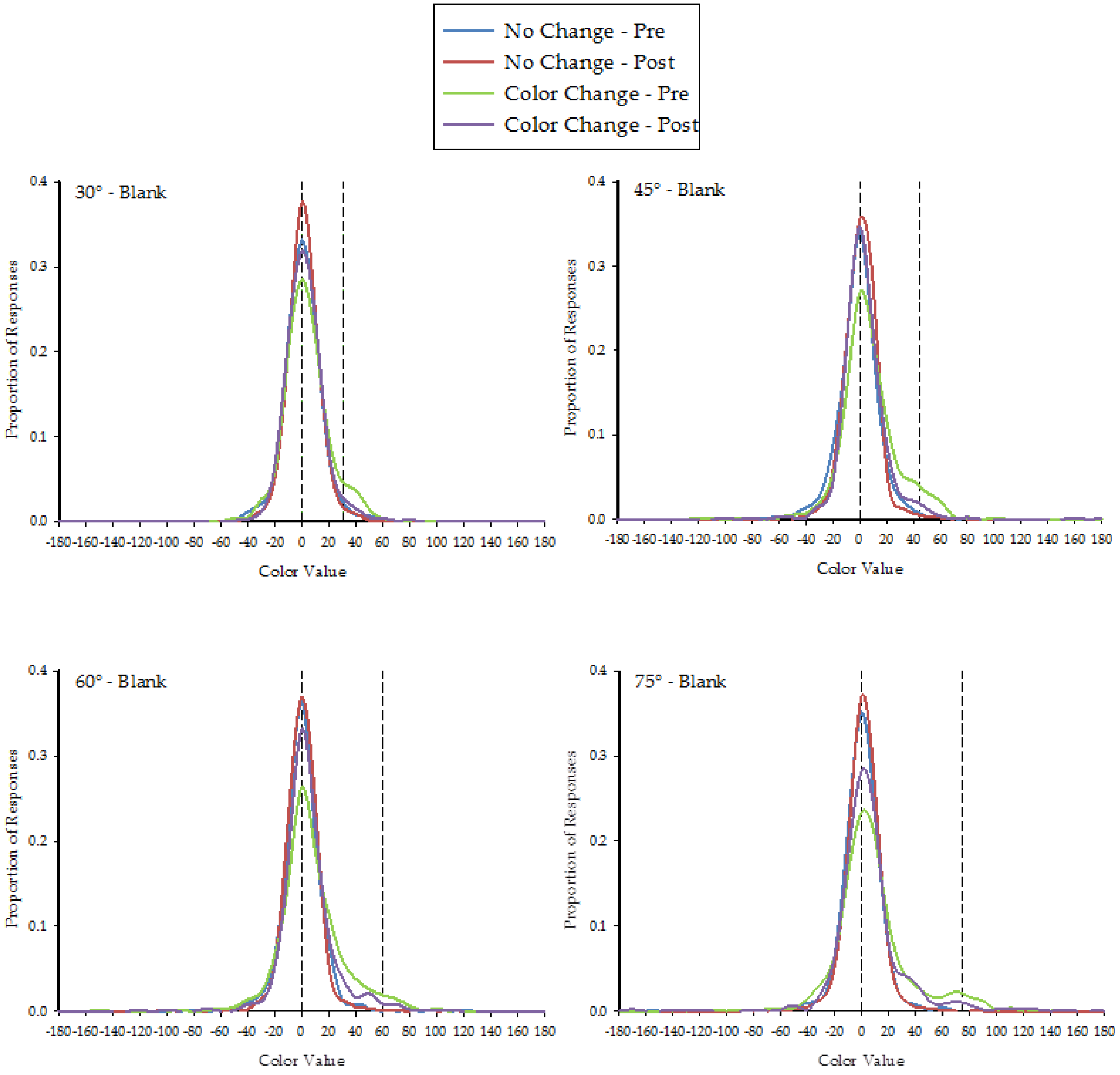

Figure 4.3. Proportion of color responses for the Instability (Blank) conditions of Experiments 3-6. The dashed lines represent the target color value at 0° and the corresponding distractor values in each experiment.

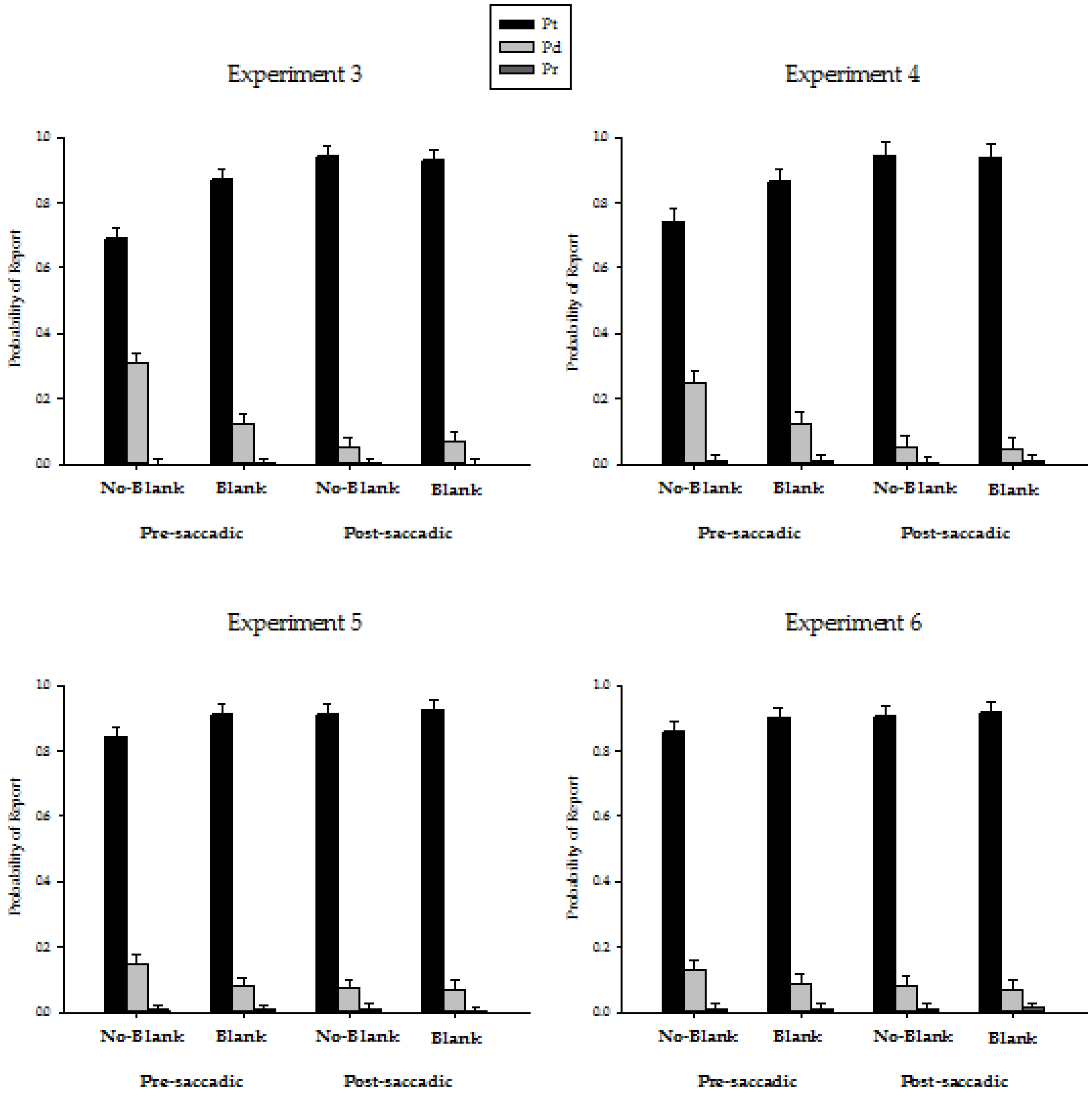

Figure 4.4. Best fits of the mixture modeling parameter estimates for the probability of reporting the target colorp_t, probability of reporting the distractor colorp_d, and probability of reporting a random color value p_r in color-change conditions of Experiments 3-6. Error bars represent 95% within-subject CIs calculated for each object (p_t,p_d, andp_r) separately (Franz & Loftus, 2012; Loftus & Masson, 1994).

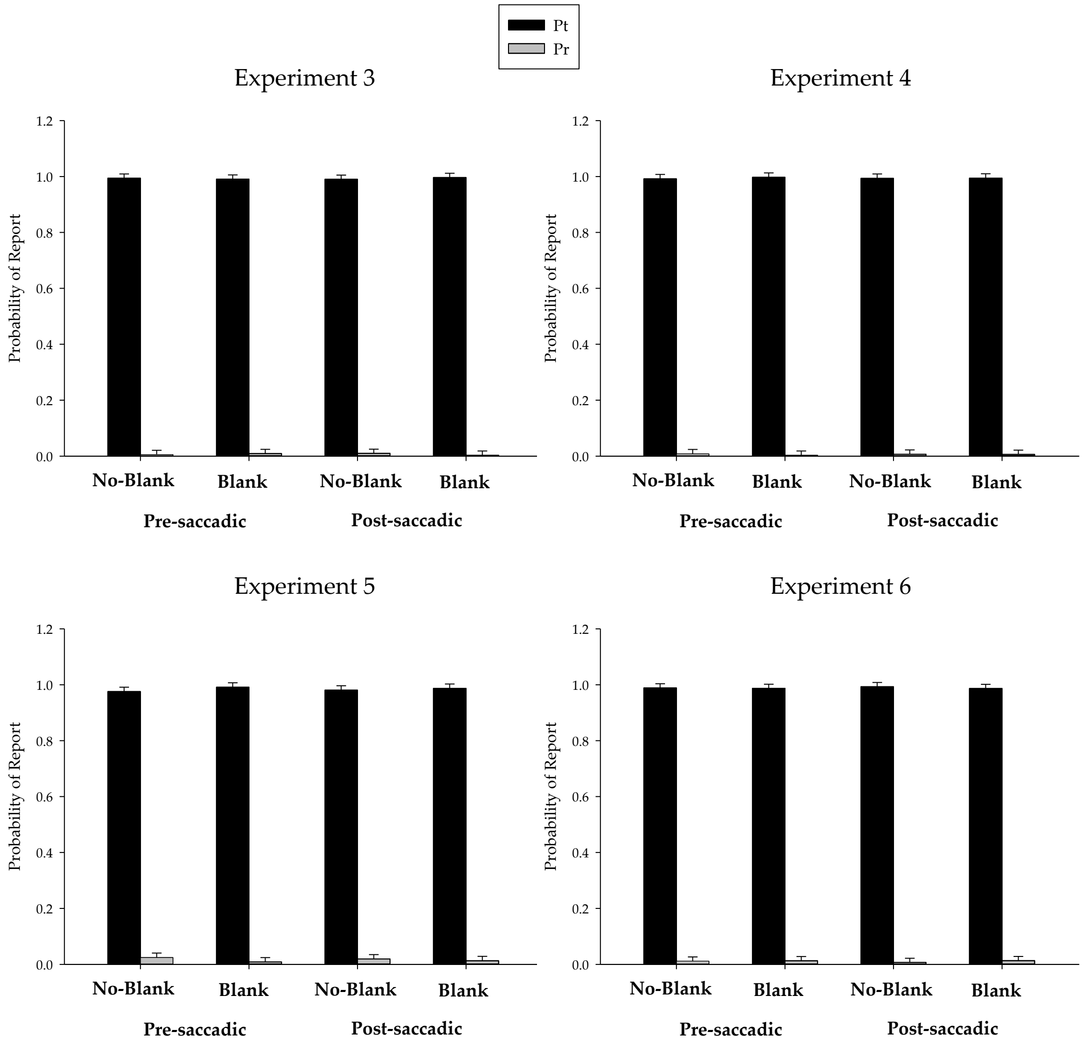

Figure 4.5. Best fits of the mixture modeling parameter estimates for the probability of reporting the target colorp_t, probability of reporting the distractor colorp_d, and probability of reporting a random color value p_r in no-change conditions of Experiments 3-6. Error bars represent 95% within-subject CIs calculated for each object (p_t andp_r) separately.

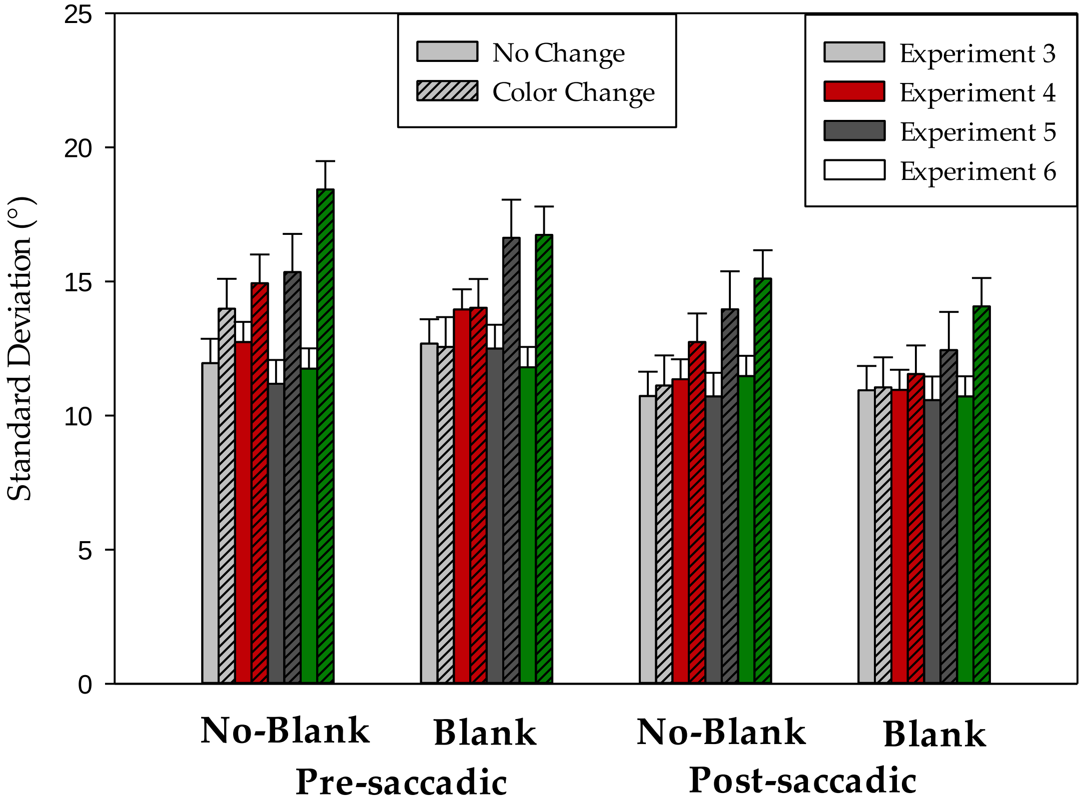

Figure 4.6. Best fits of the mixture modeling parameter estimates for the standard deviation of the target distributions (in degrees) in no-change (solid) and color-change (striped) trials in Experiments 3-6. Error bars represent 95% within-subject CIs based on the color change conditions of each experiment.

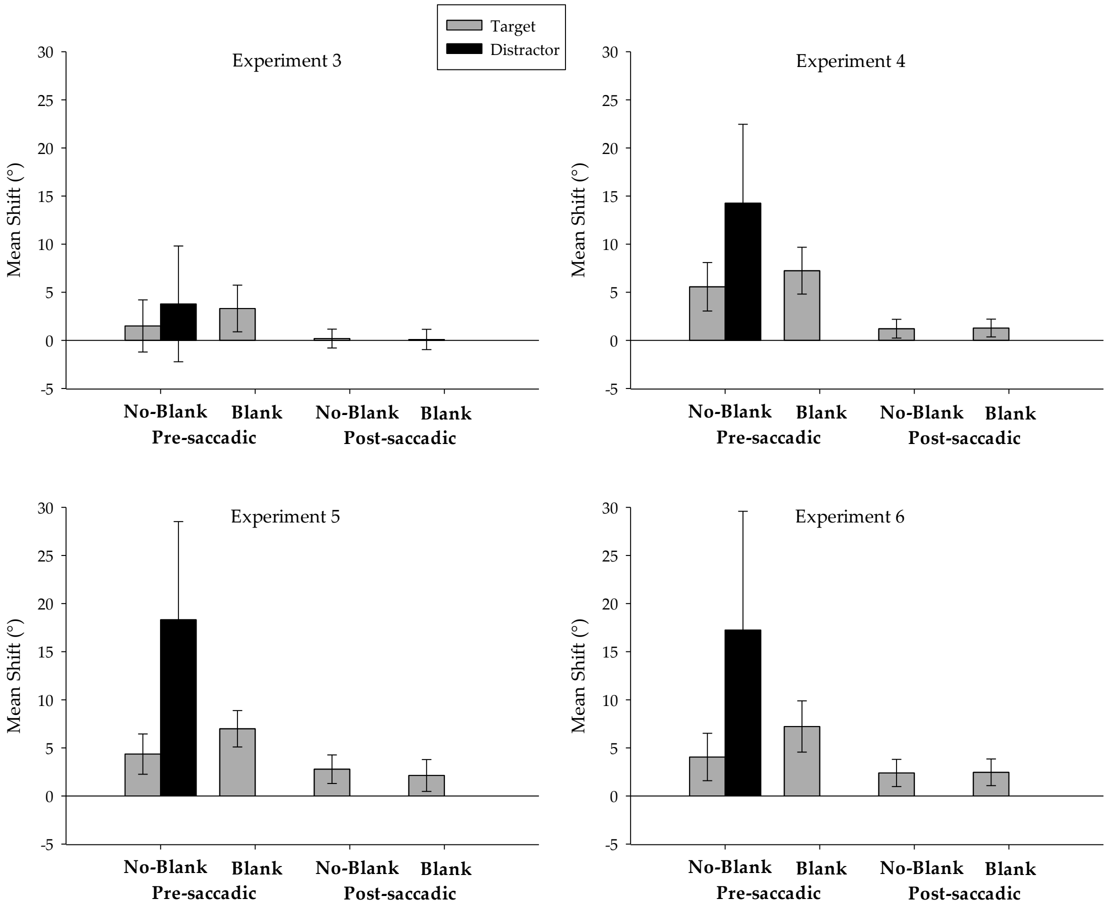

Figure 4.7. Mean shift (in degrees) in target and distractor distributions of Experiments 3-6. Positive values indicate a shift toward the unreported color. Specifically, a positive shift for the target distribution means that the mean was shifted toward the distractor color while a positive shift for the distractor distribution means that the mean was shifted toward the target color. Error bars represent 95% CIs calculated for each condition separately.

CHAPTER V

GENERAL DISCUSSION

Transsaccadic stability and updating

Phenomenological experience of the visual world is continuous, even though the input the visual system receives is frequently disrupted by our eye, head, and body movements. The visual system's remarkable ability to establish visual stability from disjointed information has been the center of transsaccadic perception research for many years.

Earlier accounts of transsaccadic stability proposed that the visual system retains detailed, high-resolution images obtained during each fixation and merges them into a single, spatiotopically organized image (Brietmeyer et al., 1982; Jonides et al., 1982; McConkie & Rayner, 1976; Wolf et al., 1978, 1980). Later studies found evidence against this type of global, image-based fusion (Bridgeman & Mayer, 1983; Irwin et al., 1988; Irwin et al., 1983), and instead determined that a comparison between the pre-saccadic information of the saccade target and the post-saccadic information at or near the saccade landing position is used to establish transsaccadic object correspondence (Currie et al., 2000; Deubel et al., 1998; Hollingworth et al., 2008).

However, studies showing that visual neurons in the primate brain shift their receptive fields before a saccade resulted in reconsideration of the global integration accounts (Duhamel et al., 1992). The key finding in these predictive remapping studies is that prior to a saccade execution, neurons will start responding for stimuli at locations that will become their receptive field after saccade completion. This predictive property of the receptive field shifts was taken evidence for both global, integration-based visual stability (Hall & Colby, 2011; Melcher, 2009) and local, comparison-based visual stability (Mathôt & Theeuwes, 2011; Wurtz et al., 2011). The global, integration-based accounts were later refuted by both behavioral (Knapen et al., 2009; Knapen et al., 2010) and neurophysiological studies (Zirnsak et al., 2014).

Together with the earlier behavioral work, these studies support an object-based mechanism of transsaccadic visual stability: The properties of the target are preferentially encoded into visual working memory prior to saccade execution, and retained across the saccade, most likely through convergence of receptive fields toward the saccade target (Zirnsak et al., 2014). After the completion of the saccade, the remembered properties of the target are compared with the post-saccadic properties. Object correspondence will be disrupted if there is a discrepancy between the pre- and post-saccadic properties (Demeyer et al., 2010a; Deubel et al., 1996; Tas, Moore, et al., 2012).

At saccade landing, when visual stability is established, the visual system is faced with another challenge. After each saccade, there are two representations of the target object: the pre-saccadic representation which is acquired peripherally and the post-saccadic representation which is acquired foveally. An integral part of transsaccadic perception is representing the target object as a persisting entity, which requires a mechanism by which the pre-saccadic state of the target object is reconciled with its post-saccadic state. In the current dissertation, my aim was to test directly the mechanisms of transsaccadic updating. When visual stability is established and the pre- and post-saccadic properties of the target object are perceived as belonging to the same object, how does the visual system update the pre-saccadic representation to reflect the post-saccadic properties?

One possible mechanism by which the target representation may be updated is complete overwriting of the pre-saccadic representation with the post-saccadic representation, as proposed by the object-mediated updating framework (for a review, see Enns et al., 2009). According to the strong version of object-mediated updating, if object correspondence is established across minor disruptions, such as a saccade, then the visual system updates the representation of the target with an object-based masking mechanism. A consequence of this representational updating is that earlier properties or the object get overwritten by later properties. If this is correct, then participants should typically report the post-saccadic features of a target when asked to report the pre-saccadic features. A second possibility is that the pre- and post-saccadic features may be merged into a single representation. As in the case of complete overwriting, the visual system would lose access to the discrete states of the pre- and post-saccadic representations, resulting in a single feature representation. However, the feature value of this single representation would lie somewhere between the pre- and post-saccadic values, with the precise value depending on the relative weighting of the pre- and post-saccadic representations in the integration process. Lastly, it is possible that the visual system is able to maintain discrete representations of both the pre- and post-saccadic states of the target object, even under conditions of visual stability. In this case, multiple, episodic feature states would be associated with the same persisting object representation. Further, it is possible that these discrete states might influence each other, resulting in altered representations of both pre- and post-saccadic features.

To differentiate these possibilities, pre- and post-saccadic representations of the saccade target object were measured separately. Participants were presented with a colored saccade target and instructed to remember its color for a later test. Participants' task was to report the color of either the pre- or post-saccadic object. To examine the interaction between the pre- and post-saccadic features, on some trials the color of the target was changed during the saccade. In addition, the continuity of the saccade target was manipulated in two ways. At a gross level, I introduced the blanking manipulation, in which the target was not visible for the early portion of the fixation after the orienting saccade. This type of blanking manipulation has been shown to reliably disrupt the perception of transsaccadic object continuity (Demeyer et al., 2010a; Deubel et al., 1996; Tas, Moore, et al., 2012). At a more fine-grained level, I manipulated visual stability with the magnitude of color change. Previous studies have shown that transsaccadic change of surface features, like contrast polarity and shape, can also interfere with object continuity (Demeyer et al., 2010a; Tas, Moore, et al., 2012). Therefore, it is plausible that a substantial color change could disrupt stability on trials where target blanking was not introduced. To determine the relationship between color change magnitude and object continuity, I ran four preliminary experiments.

In Experiments 1A and 1B, the perception of object continuity was measured with the transsaccadic displacement detection task (Bridgeman et al., 1975). On each trial, participants were instructed to execute a saccade to a peripheral target disk. After the initiation of the saccade, the target was displaced either in the same or opposite direction. The task was to indicate the direction of this shift. Previous studies have shown that participants are often insensitive to even large target displacements unless the target continuity is disrupted (Demeyer et al., 2010a; Deubel et al., 1996; Tas, Moore, et al., 2012). In Experiment 1A, the magnitude of color change between the pre- and post-saccadic objects was 15 °, 30°, 45°, or 60°. Displacement direction performance in these color change trials was compared against the trials in which the target remained the same color throughout the trial (control condition). Experiment 1B was the same as Experiment 1A, except that the color change between the pre- and post-saccadic disks was 30°, 45°, 60°, 75°, or 90°. The results of Experiments 1A and 1B showed that compared to the control condition, displacement direction reports were significantly more accurate when the color change was 60° or greater. This suggests that object continuity is more likely to be disrupted if the color values of the pre- and post-saccadic states are approximately 60° apart. As discussed in Chapter 3, this finding does not indicate that color changes less than 60° never disrupt object continuity. It merely suggests that disruptions created by color change alone become more frequent at magnitudes of approximately 60° or more, and smaller change magnitudes, like 45° and 30°, have minimal effects on the probability of disrupting visual stability.

Next, in Experiments 2A and 2B, I tested whether the disruption created by the color change manipulation is as strong as the disruption created by blanking the target object. To test this, both color change and target blanking conditions were fully crossed. The magnitude of color change was 45° and 60° in Experiments 2A and 2B, respectively. The task was again to report the direction of the target shift. The results replicated Experiments 1A and 1B: 45° of color change increased detection performance but this increase was not statistically significant, but there was a trend in Experiment 2B. More importantly, participants' direction reports were significantly more accurate when the target was blanked compared to when its color was changed in both experiments, suggesting that blanking creates significantly stronger disruptions in object continuity than color changes up to 60°.

Experiments 3-6 tested the main question of the current dissertation: What is the mechanism by which object representations are updated across the saccades? To investigate this, I used a continuous report task in which participants were directly asked to report the color of either the pre- or the post-saccadic object by clicking on the appropriate color value on a color wheel (see Figure 2.1.). To date, the specific mechanisms of transsaccadic updating and the effect of transsaccadic visual stability on the representations of pre- and post-saccadic objects has not been examined. For this reason, I tested several plausible hypotheses discussed above (also see Chapter 2).

The specific predictions were grouped into three sets. The first set of predictions was motivated by the object-mediated updating framework (for a review, see Enns et al., 2009). According to object-mediated updating, if visual stability is established, then the pre-saccadic properties of the target object are likely to be overwritten by the post-saccadic properties. Therefore, under conditions of stability, there will be trials in which the pre-saccadic properties will be inaccessible, leading participants to incorrectly report the post-saccadic color. In contrast, when stability is disrupted with a blank, the pre- and post-saccadic objects will be perceived as separate objects, resulting in protection of the pre-saccadic features from being overwritten. For most of these blank trials, participants should be able to accurately report the pre-saccadic color. The second set of predictions concerns the integration of the pre- and post-saccadic representations, resulting in the loss of the precise values of both representations. This feature integration hypothesis predicts that the pre- and post-saccadic color values will be merged into a single representation, resulting in participants reporting a color value that is between the pre- and post-saccadic value. Lastly, the multiple states hypothesis predicts that participants can successfully access to both pre- and post-saccadic color. If this is true, then it is also possible that these discrete states might affect each other, resulting in the means of both pre- and post-saccadic response distributions to be shifted from their actual values.

The results provided no direct support the feature integration hypothesis (see Figures 4.2 and 4.3). The response distributions for the pre- and post-saccadic color values were clearly distinct from each other, and there was no evidence of averaging or merging of the two colors in any of the conditions across four experiments. To test the overwriting hypothesis, probabilistic mixture models were used to examine the probability of reporting the post-saccadic color when probed to report the pre-saccadic color. I ran a set of models where the means of the pre- and post-saccadic distributions were set as fixed parameters. As converging evidence, I also ran unimodal and bimodal models separately for each condition to check whether data from each condition could be better explained by a unimodal or a bimodal distribution.

When visual stability was established (no-blank condition), the pre-saccadic color was replaced by the post-saccadic color on approximately 1/3 of the trials, rejecting the strong overwriting hypothesis but consistent with a partial overwriting hypothesis. This partial overwriting result was further supported by the bimodality tests such that no-blank/pre-saccadic data were better fit by a bimodal than a unimodal model. The frequency of overwriting significantly decreased when object continuity was disrupted by a blank, indicating that the properties of the saccade target was protected from being updated. In line with this finding, blank/pre-saccadic data were better fit by a unimodal than a bimodal model. There was no significant difference between the no-blank and blank trials for the standard deviation parameter, suggesting that stability only modulates the probability of reporting the feature of the saccade target not its precision.

The data were consistent with partial overwriting, but on the majority of trials, the results indicated that participants maintained multiple representations of the saccade target properties. The final set of tests concerned whether these representations interacted with each other. The means of the pre- and post-saccadic distributions were shifted toward each other regardless of the visual stability manipulation. Further, similar mean shifts were observed in each experiment, indicating that the magnitude of color change does not modulate the strength of this interaction. Together, the present results showed two main mechanisms of transsaccadic updating: partial overwriting and feature interactions between two discrete states. In the following sections, I first review different conceptualizations of transsaccadic memory, and discuss the implications of the present dissertation for those modes. Then, I discuss how the present findings relate to the object-mediated updating framework.

Transaccadic memory

The results of the current dissertation add to our understanding of how visual system represents the visual world across saccades. Imagine you are sitting on your desk at work, looking for your red pen to grade some assignments. There are multiple objects on your desk and you make multiple saccades until you finally locate the pen. What is the representation of your desk after each saccade? Would you accumulate low-level feature information about the objects on your desk as you execute each saccade, leading to a detailed representation of the desk? Our phenomenological experience feels like we would.

Initial accounts of memory across saccades, or transsaccadic memory (TSM), were consistent with our personal experience of the world. As discussed before, several researchers proposed that the visual system retains detailed, high-resolution images obtained during each fixation and merges them into a single, spatiotopically organized percept (Banks, 1983; Brietmeyer et al., 1982; Jonides et al., 1982; McConkie & Rayner, 1976; Wolf et al., 1978, 1980) which was later rejected in favor of the object-based view (Irwin, 1991; Irwin et al., 1988). Further, transsaccadic change detection studies have also shown that high-resolution images are not retained across saccades (Bridgeman & Stark, 1979; Grimes, 1996; Henderson & Hollingworth, 1999, 2003).

This difficulty to detect changes across the saccades led some researchers to argue against the existence of TSM altogether (O'Regan, 1992; O'Regan & Noe, 2001). According to this view, the visual system does not store any information about the objects across the saccades because the external world itself serves as "memory". Thus, the visual system creates a new representation of the visual world during each fixation, which will then be replaced with another one after each saccade. Contrary to this view, some changes to the objects may be detected, especially if the object is attended before the eye movement. For instance, Henderson and Hollingworth (1999) presented participants with naturalistic scene images and instructed them to inspect the scenes for a memory test while also trying to detect any changes that may occur. Two possible changes could occur: The target was either rotated 90° or deleted from the scene. In addition to the nature of the change, the authors also manipulated the time point at which the change occurred. In one condition, it was during the first saccade to the object (toward) and in the other it was during the saccade right after participants fixated the object the first time (away). The results showed that participants usually missed both types of change, although the deletion of the object was more easily detected than a change in its orientation. Interestingly, the probability of detection also depended on the direction and the length of the saccade. Specifically, more deletion changes were detected if the saccade was directed toward the target object. Further, detection performance was also improved if the target object was close to the saccade landing position. These results indicate that not all information about the objects is lost across saccades.

To determine the types of information which survive across saccades, studies have extensively used the extrafoveal preview benefit method. In this method, participants are asked to execute a saccade to a location and identify a target object (usually by naming it) that appears at the saccade location (Henderson, Pollatsek, & Rayner, 1987). Object identifications are faster if the target object was presented at the saccade location before the initiation of the saccade compared to when its preview was not available. This preview benefit can be modulated by manipulating the visual similarity between the target and preview object. For instance, significantly greater preview benefits were found if the preview was identical to the target object compared to if it was a mirror image of the target (Henderson & Siefert, 1999), or if it was an object from the same basic-level category as the target (Henderson & Siefert, 2001; Pollatsek, Rayner, & Collins, 1984). It is important to note that these studies do not suggest that sensory information about the objects is retained. Rather, these effects appear to reflect the retention of post-sensory visual information, a property of visual working memory (for a review of this distinction, see Irwin, 1992c). For instance, rather than point-by-point iconic shape of an object, the visual system encodes and retains the structural information about the objects across the saccades (Carlson-Radvansky, 1999; Carlson-Radvansky & Irwin, 1995).

These findings suggest that low-level, highly detailed features about objects are not retained across saccades as initially proposed. Instead, TSM consists of more abstract visual representation(Henderson, 1997; Irwin, 1996). Further, studies have found that TSM has a capacity of three to four integrated objects (Carlson, Covell, & Warapius, 2001; Irwin, 1992a; Irwin & Andrews, 1996; Irwin & Gordon, 1998; Prime et al., 2007). In close examination, TSM and VWM share similar properties (for a review, see Hollingworth et al., 2008). Indeed, several researchers proposed that TSM is not a separate, special mechanism for transsaccadic representation of information but instead depends on VWM (Hollingworth et al., 2008; Irwin, 1992a; Prime et al., 2007).

Although the large majority of studies have indicated that transsaccadic memory retains relatively high-level visual representations, recent studies have provided a revival of the idea that low-level, iconic representations of the objects are sometimes retained across saccades (De Graef & Verfaillie, 2002; Demeyer, De Graef, Wagemans, & Verfaillie, 2009, 2010b; Germeys, De Graef, Van Eccelpoel, & Verfaillie, 2010). According to this account, TSM has two distinct components. The first component is VWM. The second component is what the authors called *the visual analog*. The visual analog is similar to iconic memory, such that it stores precategorical information of the objects and is a high-capacity, fast decaying, and maskable storage. Using the blanking method, Germeys and his colleagues (2010) found that change detection performance for a letter saccade target was almost perfect when the screen was blanked. More importantly, change detection for the blank trials also increased compared to no-blank trials for letters other than the saccade target if the location of the target letter was cued at the end of the saccade. This latter finding was taken as evidence for the existence of a high-capacity store. Additional experiments showed that the contents of this store are fast-decaying and maskable, both properties of iconic memory.

The results of the present dissertation are more consistent with the view that the information retained across the saccades depends on VWM, rather than on storage in a visual analog representation. Specifically, on a majority of trials participants had no difficulty reporting the pre-saccadic color of the target object, despite the fact that it was immediately followed by the post-saccadic color. These pre-saccadic color reports were accurate even in Experiment 3, where the probability of color change disrupting object continuity was minimal. If TSM depends on a short-lived, maskable visual analog, then the pre-saccadic color should have been masked by the post-saccadic color on every trial, resulting in an inability to report the pre-saccadic value. This was not the case. Further, trials in which the target color remained the same resulted in significantly smaller standard deviations than trials in which the target color was changed. That is, the memory of the target's color was more precise when only one color was associated with its representation compared to when two colors were associated. This finding agrees with previous studies showing that the precision of items in VWM decreases as the number of memorized items increases (Anderson & Awh, 2012; Bays et al., 2009). Thus, in the context of the present study, the information functional in performing the task was not susceptible to low-level masking, and was encoded in a resource-limited memory system, a result that is more consistent with the object-based accounts than the image-based accounts.

Object-mediated updating

Although participants could retain the color of the pre-saccadic state with no difficulty on a majority of trials in Experiments 3-6, there was also evidence for an overwriting mechanism. When the magnitude of color change was small, participants incorrectly reported the post-saccadic color on about 25-30% of the trials. For larger color change magnitudes, this proportion decreased to 15%, but importantly was not eliminated. This finding that the initial state of the target is replaced by its later state is consistent with the object-mediated updating framework (Enns & Di Lollo, 2000; Enns et al., 2009; C. M. Moore et al., 2007). Previously, object-mediated updating has been used to explain various situations that depends on establishing object continuity, such as the standing wave illusion (Enns, 2002; Hein & Moore, 2010), flash-lag illusion (C. M. Moore & Enns, 2004), motion deblurring (C. M. Moore et al., 2007, see Chapter 1 for the details of this study), response priming (Lleras & Enns, 2004), and object substitution masking (Enns, 2004; Lleras & Moore, 2003; C. M. Moore & Lleras, 2005; Pilling & Gellatly, 2010) .

The strong version of the object-mediated updating was not supported by the current findings. Rather, the infrequent occurrence of overwriting may indicate that at least in the context of transsaccadic updating, overwriting is a probabilistic mechanism, not an automatic one. It is possible that the probability of overwriting depends on the demands of the task. That is, in the current experiments, participants may have been encouraged to retain discrete representations of the two objects, potentially minimizing cases of overwriting. First, participants were explicitly told to remember the color of the pre-saccadic object for a later memory test. Thus, they were given an incentive to encode the color with high precision. In everyday scene viewing, observers usually do not explicitly try to remember the precise features of each saccade target. Instead, it may be more efficient to delay the precise feature encoding until the target object is fixated. Second, although the timing of the post-saccadic object was controlled, I did not restrict the timing of the pre-saccadic object. That is, participants had as much time as they needed to encode the color of the pre-saccadic object[6]. In natural vision, the purpose of VWM across saccades is not to encode the target with high precision but to represent the target across saccades for the purposes of later comparison. Therefore, the memory for the saccade target might be less precise outside the laboratory and more prone to being replaced by the high-quality foveal information. For these reasons, overwriting might occur more frequently and maybe automatically in more naturalistic environments than found in the current experiments. Future studies should use designs that more closely mimic the conditions of natural vision.

Further, in the current experiments, the perception of visual stability and instability were not directly measured. It is likely that the participants perceived instability on some of the no-blank trials or stability on some of the blank trials, which may have altered the probability of overwriting. One way to overcome this problem is to ask participants if they perceived one or two objects on each trial. Such instructions, however, would possibly bias participants to perceive two objects on most of the color

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[6] The mean saccade latencies on no-blank trials in which participants reported the pre-saccadic color were 227 ms, 198 ms, 216 ms, and 231 ms in Experiments 3-6, respectively. For each experiment, I correlated saccade latency with accuracy of color report. The results showed no systematic relationship across experiments. Therefore, this explanation seems unlikely.

change trials. Future work should include designs which integrate phenomenological reports of stability with perceptual reports to determine whether these two measures correlate with each other.

The results of the shifting models indicate that even when overwriting occurs, the final perception of the target object is influenced by the initial properties. For trials in which participants incorrectly reported the post-saccadic color, the color reports were shifted toward the pre-saccadic color value. In addition, significant shifts toward the pre-saccadic color were also observed even when object continuity was disrupted. Further, the post-saccadic color also affected the pre-saccadic reports, indicating a dynamic and bi-directional interaction between the pre- and post-saccadic properties. These findings suggest that information obtained prior the saccade affects the perception of the objects after fixation. Likewise, information obtained after the saccade also affects the memory of the pre-saccadic representation. Thus, even when discrete states of the object cannot be accessed, their precise features affect each other's representation, further supporting the multiple states hypothesis.

Conclusion

The present study was the first to provide direct evidence for the mechanisms by which the visual system updates representations of the objects across disruptions to enable perception of a persisting visual scene. Across four experiments, I found two main sources of updating: partial overwriting and feature interactions. Although the experiments here focused on transsaccadic perception and updating, the same mechanisms may be functional in situations where the visual system needs to establish perceptual continuity and stability when encountered with discontinuous input. Future research should examine the generalizability of these mechanisms across different types of perceptual discontinuity.

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